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ASPECTS OF THE ECOLOGY AND BEHAVIOUR OF A BREEDING POPULATION OF DIPPERS (*CINCLUS MEXICANUS*: PASSERIFORMES) IN SOUTHERN ALBERTA

by

© DAVID MICHAEL EALEY

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Aspects of the ecology and behaviour of a breeding population of Dippers (Cinclus mexicanus: Passeriformes) in southern Alberta" submitted by David Michael Ealey in partial fulfilment of the requirements for the degree of Master of Science.

....

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Date June 16, 1977

ABSTRACT

Aspects of the ecology and behaviour of a breeding population of Dippers were studied in 1975 and 1976 within the Eastern Slopes of the Rocky Mountains in southwestern Alberta. Major emphasis was placed on examining nest site distribution and selection, food availability and use, and the distribution and function of territories.

The breeding population on 41 km of stream was 45 in 1975, and 43 in 1976 of which 71 and 81%, respectively were colour-banded. Sex ratios were equal throughout the breeding season.

Mean clutch size was 4.3. Fledging success was 1.04 and 1.38 young per adult in 1975 and 1976, respectively.

As the result of juvenile mortality and dispersal no young produced in 1975 returned to breed on the study area in 1976, although one was observed to breed upstream of the study area. Annual adult mortality was 56%.

Dispersion of Dippers was observed to be clumped throughout most of the breeding and post-breeding season. Associations were a result of the monogamous, territorial breeding system during much of the summer, however, some post-breeding associations involved moulting residents and juveniles. Late fall clumping was associated with water that remained open during the winter.

The distribution of nest sites was irregular and frequently clumped because of the nature of nest site requirements. Several characteristics of nest sites were examined and sites used were in general noisier, on stabler substrate, less accessible and closer to fast water than nest sites that were not used during this study. Twenty-two artificial nest sites were created, half with nest material and half without. Dippers selected traditional sites over the artificial ones, although two artificial sites did attract Dippers. Nest material was not a cue to Dippers in nest site selection. Nest site use was shown to depend also upon site fidelity of previous occupants, timing of arrival on the study area and extent of established territories.

Food levels, based on samples of benthic organisms, were highest at the time of arrival and the time of peak feeding of nestlings. Stomach content analysis indicated that Dippers fed upon the larger, more conspicuous stream bottom invertebrates. Dippers were shown to have a number of foraging maneuvers and that the use of such maneuvers varied between pairs in different territories and with individuals.

Sizes of territories ranged from 670 to 3910 m long. Mean sizes on different streams differed: 1406 m on the Sheep River, 1473 m on Gorge Creek and 2070 m on Dyson Creek. These territory sizes were significantly larger than other territories reported for the American Dipper. Territory size was not related to mean food biomass at stations sampled within the territories, nor to features of stream morphometry.

Removal of resident pairs on parts of the Sheep River resulted in replacement by more than the original number of residents. These replacement individuals were capable of breeding. The criteria necessary to show the occurrence of a non-breeding surplus, excluded from breeding through social behaviour of residents, are discussed. A case is made for provision of extra nest sites and foraging habitat, in the event of floods, as ultimate factors causing the evolution of this social behaviour mechanism which determines breeding population numbers.

"You cannot step twice into the same river; for fresh waters are ever flowing in upon you."

From Plato's Theaetetus

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INTRODUCTION

The Bird

The American Dipper (*Cinclus mexicanus*) has had enduring appeal for naturalists because of its remarkable association with fast-running mountain streams, waterfalls, and rapids (Muir 1894). Other passerines such as Winter Wrens (*Troglodytes troglodytes*), Wagtails (*Motacilla* spp.), Western Flycatchers (*Empidonax difficilis*), and Aquatic Forktailed Chats (*Enicurus* spp.) are commonly associated with streams; however, none has the restricted habitat, nor the specialized aquatic habits characteristic of the American Dipper (Thomson 1964, Sullivan 1973).

The American Dipper is the only North American representative of the monogeneric family Cinclidae. This family, holarctic and neotropical in distribution, includes four species according to Greenway and Vaurie (1958). The distribution of the European Dipper (*Cinclus cinclus*) extends throughout Europe, to Central Asia, to small regions of north-western Africa and to southern slopes of the Himalayas (Dementiev and Gladkov 1954, Peterson et al. 1967). Some overlap occurs in the Himalayas between the distributions of *C. cinclus* and the Brown Dipper (*C. pallasii*). The latter species is also distributed throughout north-eastern Asia and into Japan. Several subspecies of the White-capped Dipper (*C. leucocephalus*) are found in the Andes of South America (Crandall 1952, Greenway and Vaurie 1958). Although Greenway and Vaurie (1958) consider C. schultzi to be a subspecies of C. leucocephalus, it may be sufficiently distinct in plumage and have a sufficiently disjunct distribution, in the mountains of northwestern Argentina, to warrant revival of the species status (Paul Handford pers. comm.). The American Dipper is confined to the mountain ranges of western North and Central America, occurring from Alaska to Guatemala (Bent 1948, A.O.U. Checklist 1957).

All species of Cinclus are closely associated with clear, rapid-running, rocky mountain streams and rarely with clear lakes near such streams (Bent 1948, Balat 1962, O'Keefe 1974). This association with mountain streams indicates the probable path of expansion of the family from a Palearctic origin, along mountain chains, to the Nearctic by crossing the Bering Strait. Therefore, it is not surprising that this genus is absent from apparently suitable habitat in eastern North America and Central Africa; these two regions are separated from areas inhabited by Dippers by vast stretches of mountainless country (Barden 1941).

Similarities, which appear to be adaptations to similar habitat, exist among the Cinclidae in roosting and nesting habits (Hann 1950, Hewson 1967, 1969, Sullivan 1973, Sunquist 1976), locomotion (Brownlow 1949, Jones and King 1952, Goodge 1959), courtship behaviour (Rankin and Rankin 1940, Bakus 1959a, Sullivan 1973) and foraging habits (Bakus 1959a, Pastukhov 1961, Mitchell 1968). Several of these similarities are discussed in some detail below.

Dippers are assumed to be non-migratory in habitat where streams do not freeze over during the winter. However, considerable portions of the streams, used during the breeding season are frozen over and as a result scattered winter movements have been hypothesized and documented: altitudinal shifts to lower, more open streams (Bakus 1959b, Balat 1962, King et al. 1973, Sullivan 1973, Price 1975) or even movements from one coastal region to another by European Dippers (Andersson and Wester 1975).

Shortly after Dippers return to the breeding areas in early spring, they establish territories along the stream. In most cases Dippers are already mated when they return to the breeding territory (Sullivan 1973, Price 1975). The pair remains entirely within the territory during the breeding season (Hann 1950, Bakus 1959a, Sullivan 1973). They forage in, above, and to some degree along the banks of the stream, eating aquatic insects, both adults and immatures, and occasionally other invertebrates and small fish (Hann 1950, Bakus 1959a, Mitchell 1968, Thut 1970, Sullivan 1973).

Nests are generally placed on rocky ledges, or ledges below bridges, directly over the water (Muir 1894, Jost 1970, Sullivan 1973, Price 1975). Sullivan (1973) describes the duration of the periods of the nesting cycle, from nest building to fledging of the young. After the young fledge they are fed by the adults for up to 2 weeks; once independence is achieved, many wander over considerable distances in the autumn (Price 1975).

Physiological and morphological adaptations of Dippers to an aquatic habitat have been studied by Crisp (1865), Balat (1960), Goodge (1959, 1960), Jones and King (1952), and Murrish (1968, 1970a, 1970b). These studies conclude that the Cinclidae show considerable convergence with other aquatic birds.

I studied Cinclus mexicanus unicolor which is the subspecies present in most of the mountain ranges of western United States and Canada (A.O.U. Checklist 1957). Its entire body is slate grey with slight brownish tinges about the head and neck; this colouration makes the birds difficult to see against rocks along streams. These Dippers are 17.5 to 21.0 cm long, weigh from 48 to 67 g (Appendix I), have chunky bodies, and a short tail that is frequently tilted upwards, somewhat like a wren's. Dense, compact plumage provides insulation and also sheds the cold water in which the bird is frequently submerged.

The Objectives

Early accounts of the breeding biology of C. mexicanus were largely anecdotal (Muir 1894, Henderson 1908, Cordier 1927, Ehinger 1930, Steiger 1940). Hann (1950), in Colorado, presented the first thorough investigation into its nesting behaviour. Bakus (1957, 1959a, 1959b) studied movements, territoriality, population density, and general life history of the species in western Montana. From observation of 24 banded individuals, 9 of which were regularly observed, Bakus was able to demonstrate altitudinal shifts by individuals in the late summer and early fall and also to determine the length of stream used as breeding territories. Sullivan (1973) described the ecological and behavioural adaptations of the Dipper to its aquatic environment, based on 4 years of fieldwork in western Montana and additional observations in southern Oregon and northern Utah.

More recently, Price (1975) investigated the population dynamics of the Dipper on a stream running through Boulder, Colorado, and determined the effect of a number of habitat and social parameters upon Dipper distribution throughout the year. He discovered polygyny among a few birds during all 3 years of his study and related the occurrence of polygyny to the distribution of available nest sites (Price and Bock 1973). Concerning the distribution and numbers of breeding Dippers, Price concluded that several major factors were interacting to affect the Dipper population: number of survivors from the previous year, nest site quality, nest site dispersion, food availability, territoriality, and weather. Sullivan (1973) had implied some of these relationships in his study, but did not present adequate quantitative evidence.

Price (1975) did not consider in depth the features involved in nest site selection, variability in food availability, the diet of breeding birds, nor did he effectively test the importance of territoriality in preventing Dippers from breeding in a particular area. I felt that an investigation of these factors would be of value in interpreting the general applicability of the conclusions of Price (1975) and Sullivan (1973).

Most studies of breeding biology of the Cinclidae have been on populations where over 50% of the nests were situated on man-made structures (Bakus 1957, Balat 1964, Hewson 1967, Jost 1970, Sullivan 1973, Price 1975). Investigation of a population in an area where such artificial structures were not used would provide comparative data to interpret more clearly the breeding requirements, particularly of nesting sites of this species.

My objectives were to (1) assess the availability and use of natural nest sites in a river system where man-made structures were present but not used, (2) record the availability of food, its actual selection by Dippers, and the behavioural responses that may occur as a result of changing food availability and individual requirements, and (3) determine the effectiveness of social behaviour in preventing Dippers from breeding in a particular area.

STUDY AREA

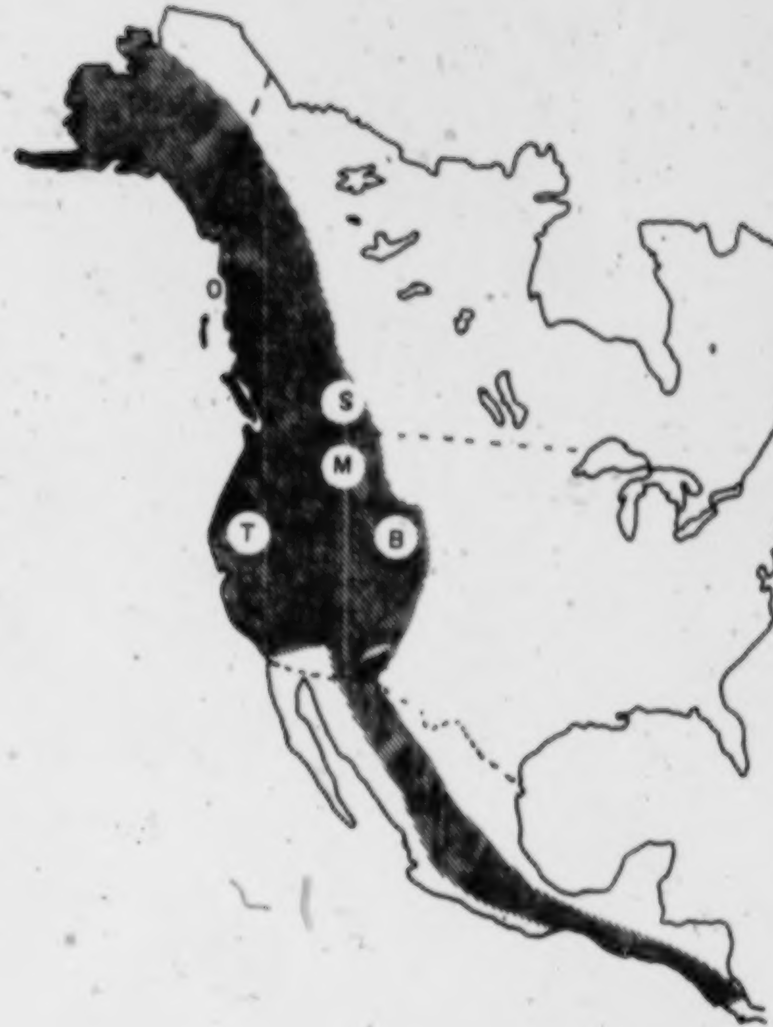
To date, this study is the first intensive investigation of the ecology of the American Dipper in Canada (Fig. 1). Like most North American studies of Dippers, the work was undertaken on the eastern slopes of the Rocky Mountains. The site is located about 45 km southwest of Calgary, Alberta.

All the streams in the study area flowed out of one drainage basin. At the upstream ends of the study area, intervening heights of land and unsuitable breeding habitat isolated the population. Dippers were found nesting 2 km downstream of the study area, and additional pairs were found nesting even further downstream. No interactions were observed between these birds and Dippers in the study population.

The study area consisted of 17 km of the Sheep River, 8 km of Dyson Creek, and 10 km of Gorge Creek (Fig. 2). Dyson Creek emptied into the Sheep River at the downstream end of the main study area, whereas Gorge Creek entered it about 2.5 km upstream from Dyson Creek. The lowest 2 km of Cliff, Junction, and Bluerock Creeks were used by breeding Dippers, so were included in the major study area; however, none of these streams was investigated as thoroughly as the other portions of the intensive study area.

This study area was suitable for many reasons. First, the R. B. Miller Biological Station, located near the center of the study area, gave easy access to the streams. Second,

Figure 1. Distribution of the American Dipper. Locations of recent studies: B -Boulder, Colorado (Price 1975); M -Missoula, Montana (Bakus 1957, Mitchell 1968, Sullivan 1973); S -Sheep River, Alberta (this study); T -Trinity County, California (M. Corilee, pers. comm.).


O
S
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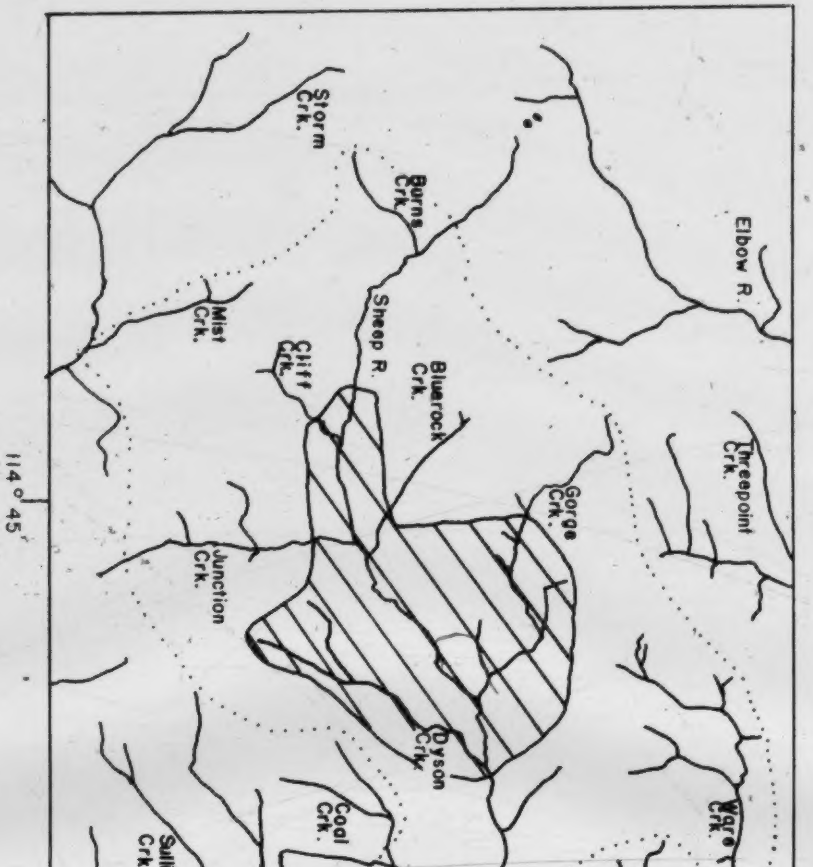
B

Figure 2. Map of the study area in southwestern Alberta. The main study area is cross-hatched and the peripheral study area is encompassed by the dotted line.


Elbow R.
Storm Crk.
Burns Crk.
Sheep R.
Mist Crk.
Cliff Crk.
Bluerock Crk.
Threepoint Crk.
Gorge Crk.
Junction Crk.
Dyson Crk.
Coal Crk.
Ware Crk.
Sullivan Crk.
March Crk.
Threepoint Crk.
Sheep R.
TURNER VALLEY
Highwood R.
1 mi
1 km
114° 45'
50° 40'

the density of the population was similar to that of two other populations studied (Sullivan 1973, Price 1975). Third, there was the opportunity to compare tributary and main river populations (Fig. 2). Lastly, the inhabited section of the Sheep River was sufficiently long to provide control and experimental areas for manipulation of the Dipper population.

Human disturbance in the study area was negligible. The nearest town, Turner Valley, was 25 km east of the downstream end of the intensive study area. This is in sharp contrast to other study areas (Balat 1964, Sullivan 1973, Price 1975) where there were habitations, dams, or water treatment plants along or near the study area, and numerous bridges over the streams.

The climate of the upper Sheep River is typical of the eastern slopes of the Rocky Mountains; it tends to be variable, but is typified by cool, moist, short summers and long, moderately cold winters with considerable precipitation. Frost has been recorded in every month of the year, although it was rare during the summer. This climatic regime is similar to that described for other North American study areas (Sullivan 1973, Price 1975).

The vegetation of the study area consists primarily of coniferous trees, although aspen (_Populus_ _tremuloides_) and, particularly, low shrubs, such as willow (_Salix_ spp.) and alder (_Alnus_ _crispa_) are often present along the stream banks. Extensive fires in the 1930's burned much of the climax white spruce (Picea glauca) forest within the watershed of the study area. This explains the present vegetative cover of uniform dense forests of lodgepole pine (Pinus contorta). Relict stands of spruce forest are found along the banks of certain sections of streams. Therefore, there are differences in vegetative cover along the banks of parts of streams. These differences are important considerations for assessing cover available to the Dippers, from both living vegetation and resulting debris. A detailed description of the vegetation of the pine forests of the study area is provided by McCourt (1969). The mixed forests are described by Boag and Sumanik (1969).

The lower 4.5 km of the Sheep River pass through moderately high (25 - 100 m) loose shale canyons. The next 4 km flow through several lower and shorter canyons of predominantly solid shale-sandstone composition. The upper 7.5 km pass between moderately high, wooded slopes with frequent sandstone outcrops; the only canyons here are narrow ones of moderate height in the uppermost kilometer of the study area. The width of the Sheep River, within the intensive study area, is from 1 m to 50 m and averages about 15 m. The depth varies from 0.2 m to 6 m. The bottom type ranges from fine shale gravel to rocky boulders occasionally larger than 1 m in diameter.

The first km of Dyson Creek, upstream of its mouth, passes through a moderately high canyon of unstable shale. The next 2.5 km pass between high, steep slopes; the southeast sides of these slopes are frequently composed of unstable shale or sandstone, and include many outcroppings. The upper 13.5 km pass mainly between densely wooded, steep slopes. A few regions of rocky outcrops and low, cliff-walled banks are found, but the majority of the banks are low, flat, wooded shelves several meters from the slopes. The width ranges from 1 m to 15 m, and averages about 5 m. The depth varies from 0.1 m to 2 m and bottom type is mostly smooth, sandstone rubble ranging from gravel-sized rocks to boulders about 1 m in diameter.

The first km of Gorge Creek, upstream from the Sheep River, passes through moderate canyons (15 - 40 m high) of fairly stable shale. The next 3 km of stream pass between numerous types of banks. There are some loose shale cliffs, but very few of these form narrow canyons. Outcrops of sandstone and stable shale are frequent along the generally low banks which in turn are flanked by steep slopes. The next 8 km passes through more open habitat with low banks and frequent meadows alongside the stream; in addition, there are infrequent stable and unstable sandstone or shale outcroppings. The upper kilometer of stream passes between slopes of unstable shale. The width varies from 0.5 m to 12 m, and averages about 5 m. The depth varies from 0.1 m to 2.5 m. The bottom type is generally composed of smaller rocks than the other streams of the study area. Most of the gravel is shale, although there are stretches of sandstone rubble. On some of the stretches, the rock diameter is up to 0.3 m.

Other streams visited were Coal, March, Burns, Ware, and Mist Creeks, as well as upstream and downstream portions of the Sheep River (Fig. 2). I searched these streams for banded birds wandering from the intensive study area, additional breeding Dippers, and nests.

METHODS

Field studies were conducted over two breeding seasons: 15 April to 22 October, 1975 and 6 April to 8 September, 1976. Preliminary work during the summer and late fall of 1974 provided a few data on population density, nest locations, and behaviour of the Dippers. Winter observations were made on December 7, 1975 and from February 24 to 27, 1976.

Most adult Dippers and a majority of the nestlings on the study area were banded with individual combinations of coloured leg-bands (Appendix I). It was necessary to distinguish individuals to obtain accurate counts of the number of Dippers on the breeding area, to determine movements of individual birds, to be certain of the number of fledglings from each nest, and to know the identity of birds holding territories. I used mist nets across the streams (Sullivan 1973) to catch the adult Dippers. In the spring of 1975 there was a period of high water that halted netting attempts on portions of the study area; as a result, some breeding birds were not banded until late in the summer, while others were never banded. A few females were caught and banded while they were incubating eggs or brooding young. One female deserted during my first field season, apparently as a result of this treatment. No desertions as a result of using this procedure were reported by either Price (1975) or Sullivan (1973).

Nestlings and adults were banded with a metal, numbered band supplied by the Canadian Wildlife Service and coloured plastic band(s) (A. Hughes Regd., 1 High St., Hampton Hill, Middlesex, TW12 1NA). Instructions from the Canadian Wildlife Service stated that colour banding of the Dippers should follow a sequence: initially one colour band placed on each bird until all combinations of band colours, on different legs and in different positions (above, below, on opposite leg) relative to the metal band, had been exhausted. Subsequently two and then three colour bands per bird were to be used. The first 36 birds were banded by this method. But, because loss of bands, as reported in another small aquatic bird, the Red Phalarope (_Phalaropus fulicarius_) (Doug Schamel pers. comm.), could lead to incorrect identification, I banded all subsequent birds with three colour bands. However, recapture of several Dippers in 1976 revealed no loss of bands. I refer herein to Dippers by the last four digits of the official band number. During this study I banded 190 Dippers (Appendix I). Band combinations of birds observed on the streams were determined usually with a pair of low-powered binoculars or a 15-power Bushnell spotting scope.

Male Dippers are indistinguishable from female Dippers in the field. Only females incubate (Sullivan 1973); therefore, observation of a banded bird incubating or bearing a brood patch permitted subsequent identification of that individual as a female, and its mate as a male. Some pairs could not be observed during the incubation period so that another method of determining sex was required. Wing lengths, tarsus lengths, and body weights were found to be different for the two sexes (Appendix II). Therefore, the sex of Dippers could be determined in the hand.

The reproductive success of each pair of Dippers was determined by periodic checks of all nests. These data on production were necessary for analysis of nest site selection, and for comparison with other studies. For each nest used by Dippers, I recorded or estimated: the dates of nest construction, laying, hatching, and fledging, as well as clutch size, hatching success and fledging success. Some of the nests were easy to reach. Other nests could only be approached using rock-climbing equipment, ladders, or a wet suit. A few nests were completely inaccessible.

Censuses of the main study area were carried out during the spring, late summer, and fall to determine the location of resident Dippers and the occurrence of transients. In 1975, the spring census involved frequent stops along the streams to catch individuals and band them; this resulted in an incomplete census at this time. Periodic censuses of adjacent streams (Fig. 2) were also made. Censuses were accomplished by: walking or wading along the stream; searching overhanging vegetation, rock ledges, and under ice ledges for hidden birds; and following birds that flew past until identification of bands could be made. This procedure was the same whether one or more workers took part in the census. Because of the possibility of some Dippers being missed if they were temporarily on any of several small tributaries entering the main streams, I regularly searched these tiny tributaries for Dippers, particularly when known residents could not be located. No Dippers were observed more than 50 m upstream on such tributaries. I am confident the censuses were accurate counts of Dippers present on the streams during the censuses.

I recorded the time, location, and activity for every Dipper observed, whether I was conducting a census or not. The locations were expressed as the estimated nearest 10 m division on the stream. This was done by locating on an aerial photograph the point where the bird was sighted and comparing this to a map with linear scale divisions of 100 m along the stream. For each banded bird, an individual history sheet was maintained that included the date, time, activity, map location, and comments for all observations.

The total number of breeding Dippers on the main study area was determined by a direct count of birds using nests. In 1975 some of the pairs were not discovered until after several days of incubation, or even after hatching; consequently, only an estimate of breeding numbers could be made that year. An accurate count of all breeding Dippers could be made in 1976, because all nest sites were known and there was greater success at banding. All Dippers found on the study area, but not observed to attempt to breed were recorded and counted as transient birds.

Nest sites were located during each census, their locations mapped, and their distribution determined. I recognized three types of nest site based upon their use by Dippers: used sites where Dippers built complete nests and continued breeding efforts; unused sites where Dippers built complete or incomplete nests that were subsequently abandoned during my study; unused sites where Dippers had nested in the past but not during my study.

I measured a series of physical characteristics at each nest site, in an attempt to determine what factors Dippers were responding to in their choice of sites. Noise, height above water, accessibility to mammalian predators, conspicuousness, nearness to fast water, and protection from wind and precipitation were features considered of possible importance to Dippers (Muir 1894, Jost 1970, Sullivan 1973, Price 1975). I devised an ordinal scale for each of several features (Table 1). Noise was assessed by standing on the bank opposite the nest site. Accessibility was estimated as the difficulty a potential mammalian predator would have in trying to reach the nest. Conspicuousness was rated from a position opposite the nest. The amount of overhang (rock ledges or vegetation) was an estimate of how well the nest was protected against wind, rain, and excessive sunlight. Water depth below the nest was estimated either directly below or nearby for nests not directly over water. The distance from the site to nearest fast water was estimated for each site as the approximate distance to a rapids,

Table 1. Ordinal classification of features noted at nest sites of Dippers.

Feature	Classification				
	1	2	3	4	5
Noise	Deafening	Very loud	Loud	Moderately loud	Quiet
Accessibility	Inaccessible to predator	Very difficult	Difficult	Slightly difficult	Totally accessible
Conspicuousness	Totally concealed	Partly concealed	Moderately visible	Visible from several angles	Obvious
Overhang	Large	Moderate	Slight	None	-
Water depth below nest	Deep (>1 m)	Moderately deep (0.5-1.0 m)	Moderately shallow (0.25-0.5 m)	Shallow (<0.25 m)	-
Distance to nearest fast water	Above rapids (or near falls)	<1 m	1 - 5 m	>5 m	-
Substrate stability	Firm	Slightly loose	Unstable	-	-

falls, or narrow chute. The stability of the substratum was assessed by the firmness of the ledge and surrounding rocks. Nest site characteristics were determined during the early spring or late fall - times at which stream conditions approximated those existing when nest site were assumed to be selected.

I wanted to test the relative importance of nest site availability on numbers and distribution of breeding Dippers. In 1975 I created 11 artificial nest sites, on each of Gorge and Dyson Creeks, by chiseling ledges and overhangs out of rock faces that appeared to fit into the range of sites chosen by Dippers. These new sites were spaced on the creeks so that there was one new nest site within 100 m of a site used by Dippers in 1975 and also one new nest site halfway between each site used in 1975. These latter artificial sites ranged from 140 m to 2 km from the traditional sites. I considered the occurrence of an old nest in a nest site a possible cue for Dippers selecting a "safe" nest site. Intact nests are evidence that the site had not been flooded and the nest washed away; the site probably had not been visited by a predator, otherwise the nest probably would have been in pieces; and the bank was stable, that is, falling rock had not covered the nest nor had the ledge collapsed beneath it. In the fall of 1975, I removed all nest material from sites used that year, on both creeks and placed these "entire" nests in all the artificial sites on Gorge Creek. This latter manipulation was designed to test the importance of the nest material as an attractant. In 1976 natural and artificial nest sites were frequently checked to determine their usage. A nest box (Jost 1970) was placed under a bridge over Gorge Creek and also supplied with parts of a nest. Numerous campers were present and quite active near the bridge, so the probability of Dipper use of the nest box was minimal. This latter effort did serve to provide an example for comparison with other studies.

As an index of food availability within the study area, I sampled (in 1976) the stream bottom fauna at a series of stations in the Sheep River, Gorge and Dyson Creeks. I used a Surber sampler (Surber 1936), with a mesh size of 1 mm, to obtain a quantitative estimate of production of invertebrates in shallow (10 to 25 cm) portions of the streams. All areas sampled were, at some time, used by foraging Dippers. The sampling procedure consisted of scrubbing and stirring the substratum, within the sampler's 1-foot square frame, to a uniform depth of about 3 cm. The samples were taken randomly at each station, within a 5 to 10 m length of stream.

Samples were taken three times during the breeding season. During the first sampling period only four samples were taken at each of the stations which were all on the Sheep River. During the latter two sampling periods all three streams were sampled and eight samples were taken per station. The number of samples/station was increased during the last two sampling periods because by making a number of cumulative samples at a station I should have been able to more thoroughly sample the diversity present (Odum 1971: 150) and increase my confidence in comparing different stations. In addition, I sampled at fewer stations in order to cover all of the streams in as short a period of time as possible; this reduced the likelihood of making collections during a major insect emergence period and thus biasing inter-station comparisons.

The Surber sampler has several disadvantages as a quantitative sampler of stream benthos (Needham and Usinger 1956, Chutter and Noble 1966, Chutter 1972), however, for the purpose of this study, and others (Sullivan 1973, Price 1975) the Surber sampler gives a suitable index of biomass for comparative purposes. These quantitative bottom samples also provide an index of flying insects around the stream, because the majority of such insects have their immature stages in the water (Hartland-Rowe and MacDonald 1961).

The stream samples were stored in 70% alcohol immediately after they were obtained. Invertebrates were separated from gravel and detritus using sugar flotation (Anderson 1959), and sorted into taxonomic and size categories to determine the diversity of invertebrates and the range of size classes available to Dippers. Samples from each station were then oven-dried for 12 hours and weighed to the nearest 0.0001 g.

In order to compare the fauna in the stream samples with that sampled by the Dippers, I examined the stomach contents of six Dippers removed from the study area. A forage ratio was determined, for taxa found in Dipper stomachs, in a similar manner to that of Mitchell (1968).

Each year I monitored fluctuations in the water depth and turbidity of Gorge Creek and the Sheep River. As further investigation into the parameters likely affecting use of the streams by Dippers, I classified features within each 100 m section of the stream travelled during the early fall census (Table 4) in 1975. In addition to searching for Dippers during this census, I estimated: percentage of stream bank covered by vegetation; abundance of exposed rocks, cover for the birds; proportion of different morphometric types in the stream, that is, channel, riffle, or pool; and availability of cliff ledges suitable for nest sites. This last estimate was considered the nest site potential for a stretch of stream.

Detailed observations of the activity of six pairs of Dippers were undertaken in 1975. Three of these pairs were observed much more frequently than the others. In 1976 observations were continued on three pairs. Varying amounts of time were spent on each pair as a result of occasional tourist and camper disturbance. One could frequently deduce what Dippers had been doing or would be doing by their behaviour upon returning to or leaving from the nesting area. Consequently, the majority of the observations took place from locations within sight of the nest. Dippers were easily disturbed or lost from sight when attempts were made to follow them and to obtain continuous records of their activity. As a result, additional observations were made from predetermined points from which the activities of birds could be recorded as they moved into the visible portion of stream. Observations were made throughout the day to attempt to determine any changes in activity over the day.

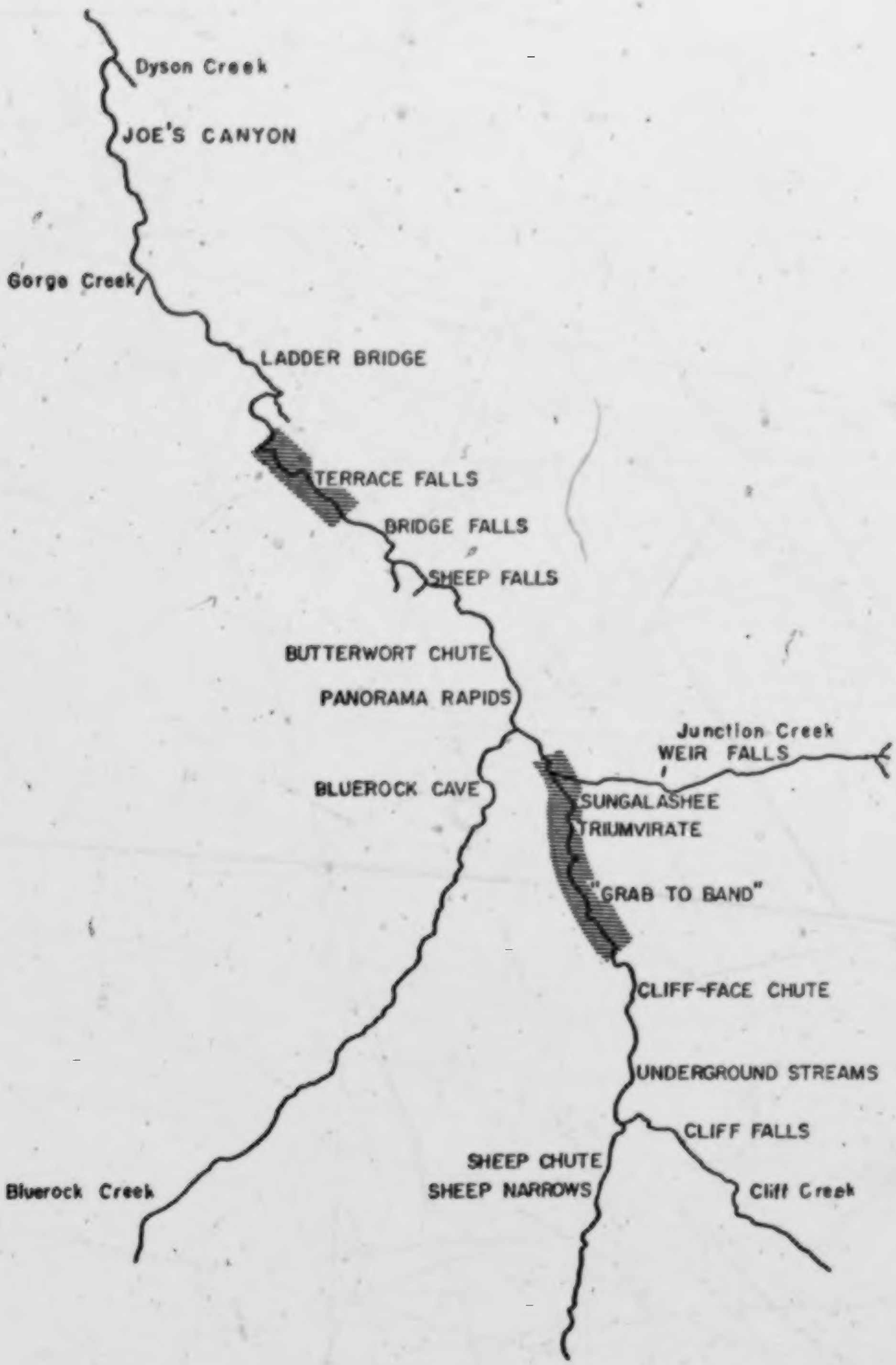
Observations of activity were recorded on tape or continuously recorded on data sheets using coded symbols for various behaviours and locations. The taped observations were transcribed into the same format as the written observations. The type of activity was recorded every 20 seconds and changes of activity during the interval between each of these points were also recorded. Wiens et al. (1970) describe a similar procedure for recording activity. The emphasis is placed herein on the foraging activities and locations, in an attempt to determine the relationship between feeding and habitat structure.

Dippers maintain breeding territories by a variety of means: singing, chasing of intruders, and aggressive postures directed towards intruders (Sullivan 1973). I estimated the length of their breeding territories to determine whether territory sizes and, indirectly, breeding numbers were influenced by parameters of food abundance, nest site availability, and physical structure of the stream.

I attempted to determine territory boundaries by watching interactions between Dippers in adjacent territories and by trying to force interactions by chasing neighbouring individuals together. This technique is recommended by Price (1975), but unfortunately was rarely possible during my study. Instead, I determined territory size by chasing resident Dippers upstream and downstream from their nest site until they reached a point from which they would fly in the opposite direction past me. If the Dipper flew past a chaser from the same point at least three times, then Price (1975) felt this point represented the boundary of the territory. I followed this procedure and usually recorded consistent "fly-backs" at presumed boundaries. In several cases, I was able to compare these responses with observations of territorial interactions and the two methods were in agreement. Some birds were chased only once to each boundary, but in these cases it was apparent that the flying back was not a response to an abrupt change in the topography, nor was it a response to an opening created when I did not follow the bird closely enough.

Dippers were removed from two portions of the Sheep River study area in 1976 (Fig. 3). This removal was designed to determine what effect the creation of vacant habitat might have on adjacent birds and whether the space would be reoccupied by non-territorial Dippers as indicated by Price (1975). As soon as Dippers began building nests in

Figure 3. Map of that part of the Sheep River located in the main study area (Fig. 2). Cross-hatched areas indicate locations where individuals establishing territories were removed in 1976. Nest sites that were used were located on the streams adjacent the names.


Dyson Creek
JOE'S CANYON
Gorge Creek
LADDER BRIDGE
TERRACE FALLS
BRIDGE FALLS
SHEEP FALLS
BUTTERWORT CHUTE
PANORAMA RAPIDS
Junction Creek
WEIR FALLS
BLUEROCK CAVE
SUNGALASHEE
TRIUMVIRATE
"GRAB TO BAND"
CLIFF-FACE CHUTE
UNDERGROUND STREAMS
CLIFF FALLS
SHEEP CHUTE
SHEEP NARROWS
Bluerock Creek
Cliff Creek

the removal areas, I removed these birds by netting or shooting. Subsequent occupants also were removed as soon as they began nest building. The possible outcomes for this experiment were: change or no change in the behaviour of adjacent territory holders and occupation or no occupation of the vacant habitat by newcomers.

RESULTS AND DISCUSSION

Stream Environment

Relatively few avian population studies have centered on riparian-dwelling species, so that this type of habitat and the abundance and availability of resources required by such birds has not reached widespread familiarity. Therefore, it is necessary to examine the resources potentially affecting the numbers and distribution of Dippers within a population. The stream environment is a dynamic one; fluctuations in water conditions (turbidity, depth, velocity) cause changes in foraging maneuvers by Dippers (Sullivan 1973, this study) and affect the success of nests (Sullivan 1973, Price 1975, this study). The structure of the stream banks determines the abundance and availability of nest sites because of the type of nest site selected by Dippers. The abundance of vegetation and rocks along the banks determines the amount of cover available, for these birds restrict their activities to the streams.

Water levels and flow rates in both Gorge Creek and the Sheep River fluctuated considerably during the seasons of 1975 and 1976 (Figs. 4, 5). Because spring runoff caused noticeable increases in water depth as a day progressed, all measurements were taken at the same time and place each day for the 2 years. In 1975 the highest peaks were as much as 100 percent higher than peaks at similar times in 1976

Figure 4. Daily readings of water depth in the Sheep River, 1975 and 1976. Depth recorded in the evening from a fixed depth gauge.

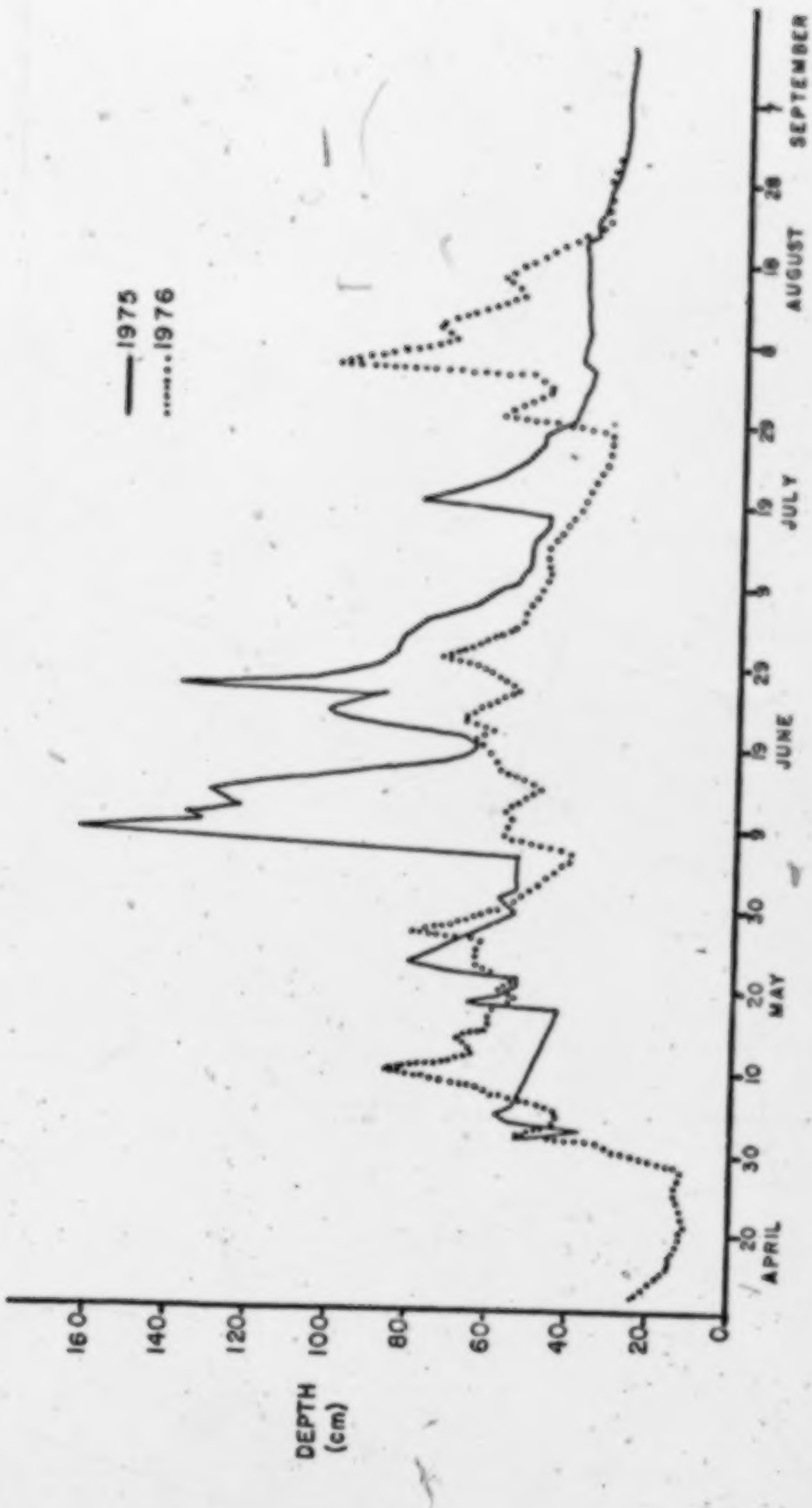
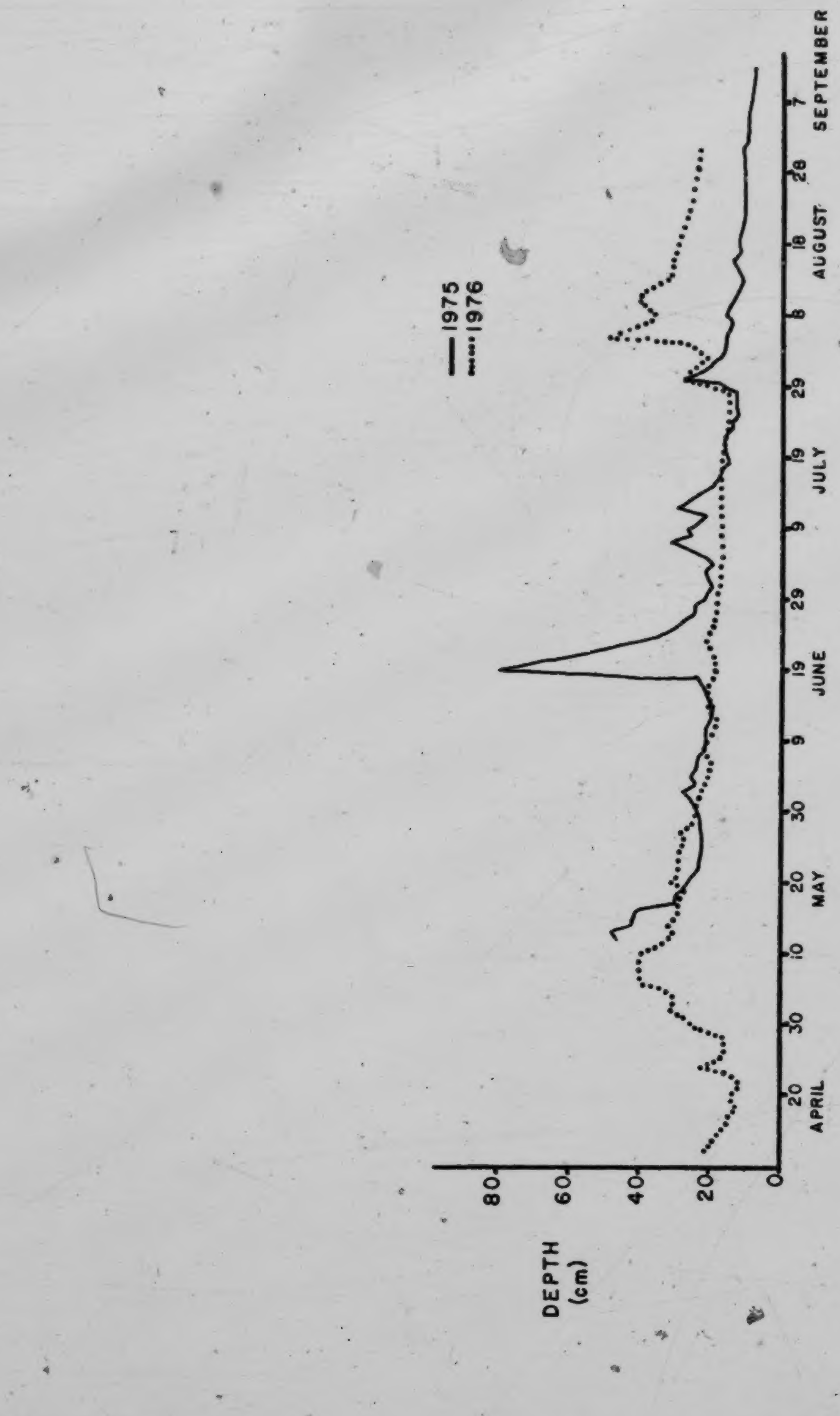

DEPTH (cm)
0
20
40
60
80
100
120
140
160
APRIL
20
30
10
MAY
20
30
9
JUNE
19
29
9
JULY
19
29
8
AUGUST
18
28
7
SEPTEMBER
1975
1976

Figure 5. Daily readings of water depth in Gorge Creek, 1975 and 1976. Depth recorded in the evening from a fixed depth gauge.


DEPTH (cm)
80
60
40
20
0
APRIL
20
30
10
MAY
20
30
9
JUNE
19
29
9
JULY
19
29
8
AUGUST
18
28
7
SEPTEMBER
1975
1976

(mid-June to early July). Until the end of June, these peaks in water level were the result of spring runoff from the snow-melt in the upper reaches of the drainage basin. The highest water levels occurred between 17 and 27 June, and between 2 and 10 July, in 1975. These two peaks resulted from a combination of late runoff and heavy rain (9.8 cm and 2.7 cm, for the two peaks respectively) which fell over a 3-to-4-day period prior to the peak. In 1976 the only major peak (between 4 and 8 August) was after most Dippers had completed breeding. At least three lesser peaks occurred during the breeding season in 1976, each of which affected stream turbidity but only one very low nest site (Butterwort Chute low site, Fig. 3). Snow accumulation over the winter of 1974-1975 was greater than in 1975-1976, which may explain the reduced effect of some spring rain storms in 1976 (exact amount of precipitation is not known for the latter period). In addition, spring break-up occurred 3 weeks to 1 month earlier in 1976 than in 1975.

Stream turbidity fluctuated with volume flow; as water level rose, the turbidity increased. Turbidity readings (Table 2) were obtained at the depth stations when water levels were recorded. Stream turbidity affected the foraging habits of Dippers (Sullivan 1973, this study) and at high levels probably affected the benthic fauna (Waters 1964, 1969). Gorge Creek was relatively clearer in 1976 than in 1975 ($X^2 = 3.176$; $0.10>p>0.05$). The Sheep River also had a higher proportion of clearer days in 1976 than in

Table 2. Relative turbidity of water in the Sheep River and Gorge Creek recorded at the depth stations in 1975 and 1976.

	Days (%)			
	Sheep River		Gorge Creek	
Relative Turbidity	1975	1976	1975	1976
Clear	41 (44)	16 (27)	12 (16)	26 (43)
Slightly murky	14 (15)	15 (25)	17 (22)	7 (12)
Moderately murky	4 (4)	11 (19)	8 (10)	5 (8)
Murky	14 (15)	3 (5)	18 (23)	2 (3)
Very murky	8 (9)	6 (10)	6 (8)	9 (15)
Muddy	12 (13)	8 (14)	16 (21)	11 (18)
TOTAL	93	59	77	60

1975 (71% versus 63%, respectively) but this was not a significant difference ($X^2 = 0.969$; $p > 0.30$).

Features of the stream bank ~~are~~ used as escape cover by both moulting (Sullivan 1973, this study) and breeding Dippers. The availability of cover is heterogeneous both in nature and distribution (Figs. 6, 7). Despite this heterogeneity, there is considerable cover of one type or another available for the Dippers; this contrasts with the situations in Colcrado (Price 1975) and Montana (Sullivan 1973) where such cover was largely lacking.

The nature of the stream bed varied along its course, particularly on the Sheep River (Fig. 8). Thus a variety of potential foraging sites existed, each requiring different foraging methods (Sullivan 1973). The nature of the banks was important in providing appropriate nesting and roosting sites. Suitable nest sites were clumped in distribution (Fig. 9). The characteristics of suitable roosting sites are similar to those of nest sites (Hewson 1969, Sullivan 1973). Cinclids have been recorded roosting at nest sites outside the breeding season (Hewson 1969, this study). Thus the distribution of these sites may be important to survival of Dippers throughout the year.

Figure 6. Extent of vegetative cover at the water edge along the banks of the streams in the main study area. No data for the Sheep River from the mouth of Dyson Creek (km 0) to mouth of Gorge Creek (km 2.5). Units of vegetative cover: 0- <5%, 1- 5-25%, 2- 25-50%, 3- 50-75%, 4- 75-100%. The south bank is upper and the north bank is lower in the figure.

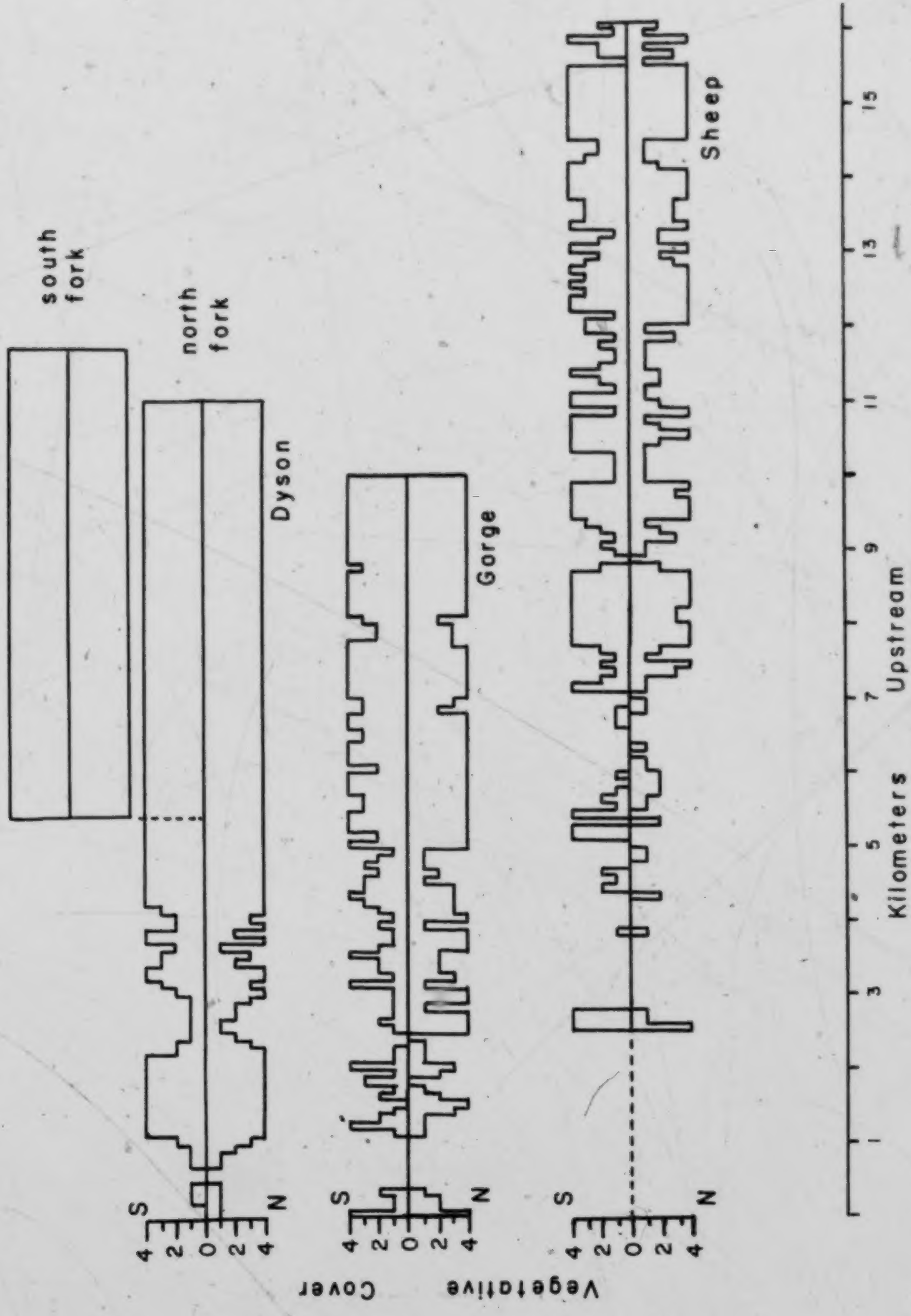

south fork
north fork
Dyson
Gorge
Sheep
S
N
4
2
0
2
4
Vegetative Cover
Kilometers Upstream
1
3
5
7
9
11
13
15

Figure 7. Amount of rock cover along the banks of the study area streams. No data for the Sheep River from the mouth of Dyson Creek (km 0) to mouth of Gorge Creek (km 2.5). Units of rock cover: 0- none; 1- poor (few rocks); 2- fair (several rocks); 3- good (abundant rocks).

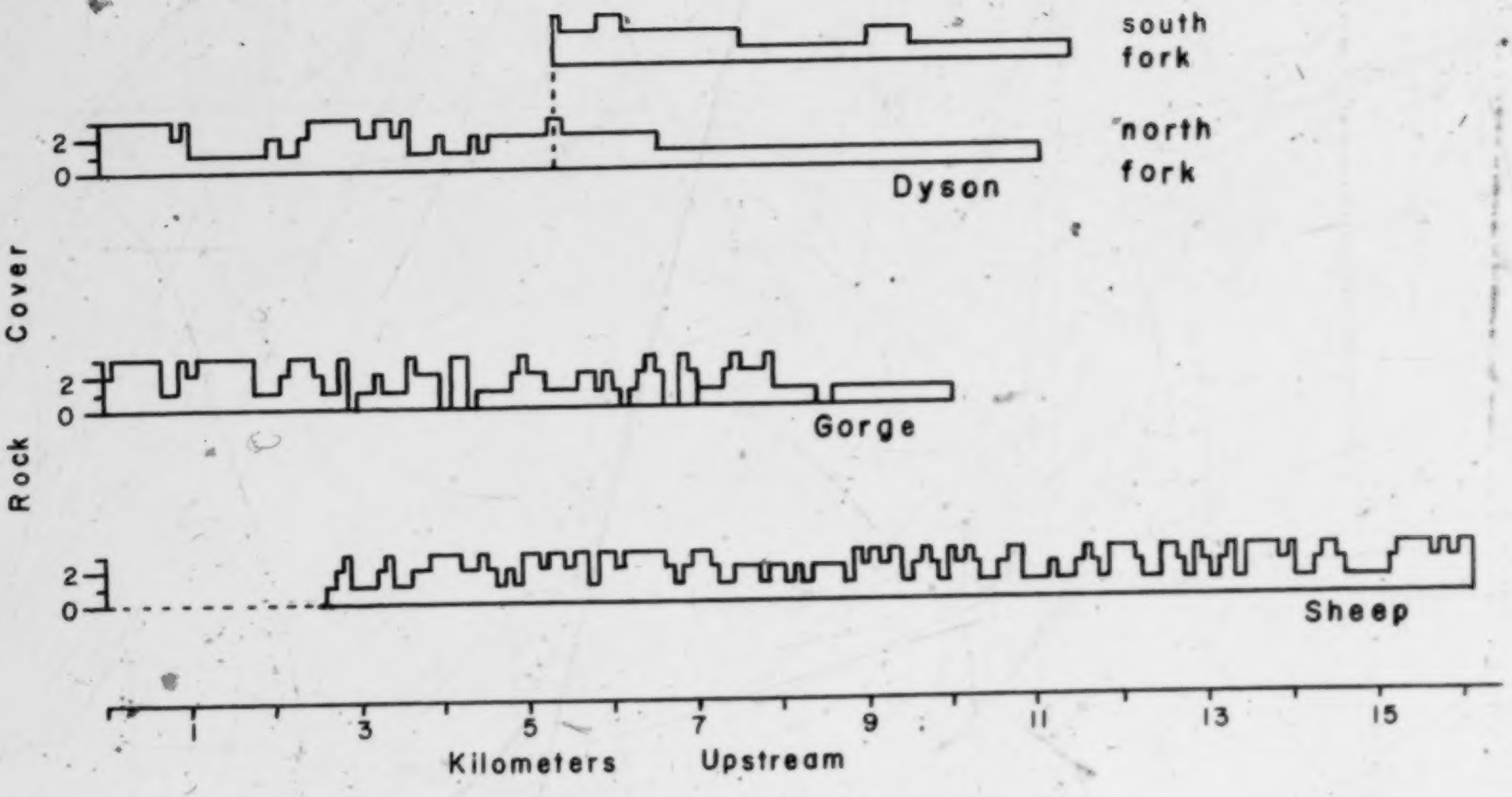

south
fork
north
fork
Dyson
Gorge
Sheep
Rock Cover
2
0
2
0
2
0
1
3
5
7
9
11
13
15
Kilometers Upstream

Figure 8. Stream morphometry of the three major study area streams. No data for the Sheep River from the mouth of Dyson Creek (km 0) to mouth of Gorge Creek (km 2.5). Categories: 0- shallow (<0.5 m) gravel or rocky beds; 1- shallow beds (>50%) and shallow, fast channels (<50%); 2- shallow channels (<1 m), pools and a few shallow beds; 3- deep channels (>1 m), pools and a few shallow beds; 4- deep channels, pools and falls.

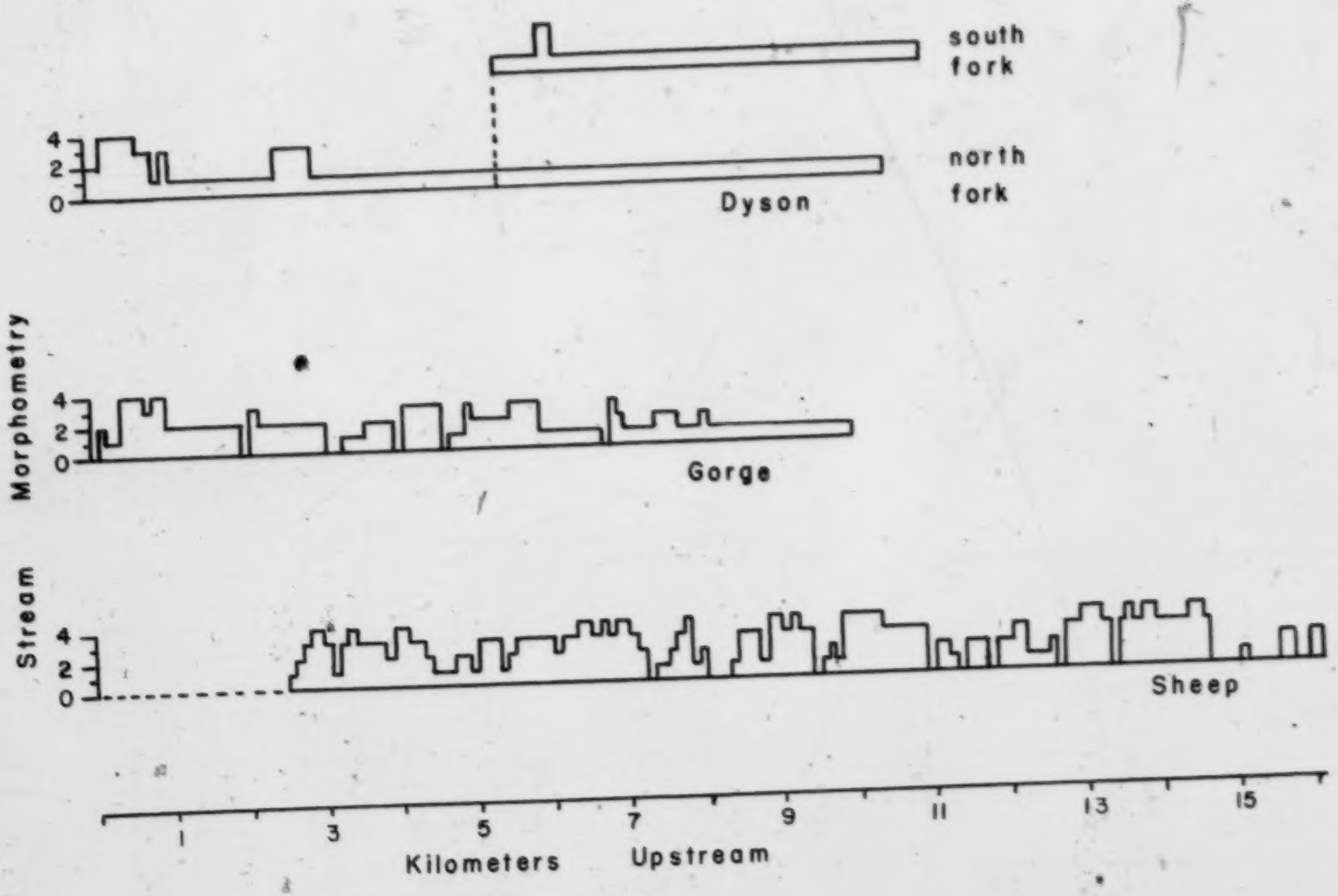
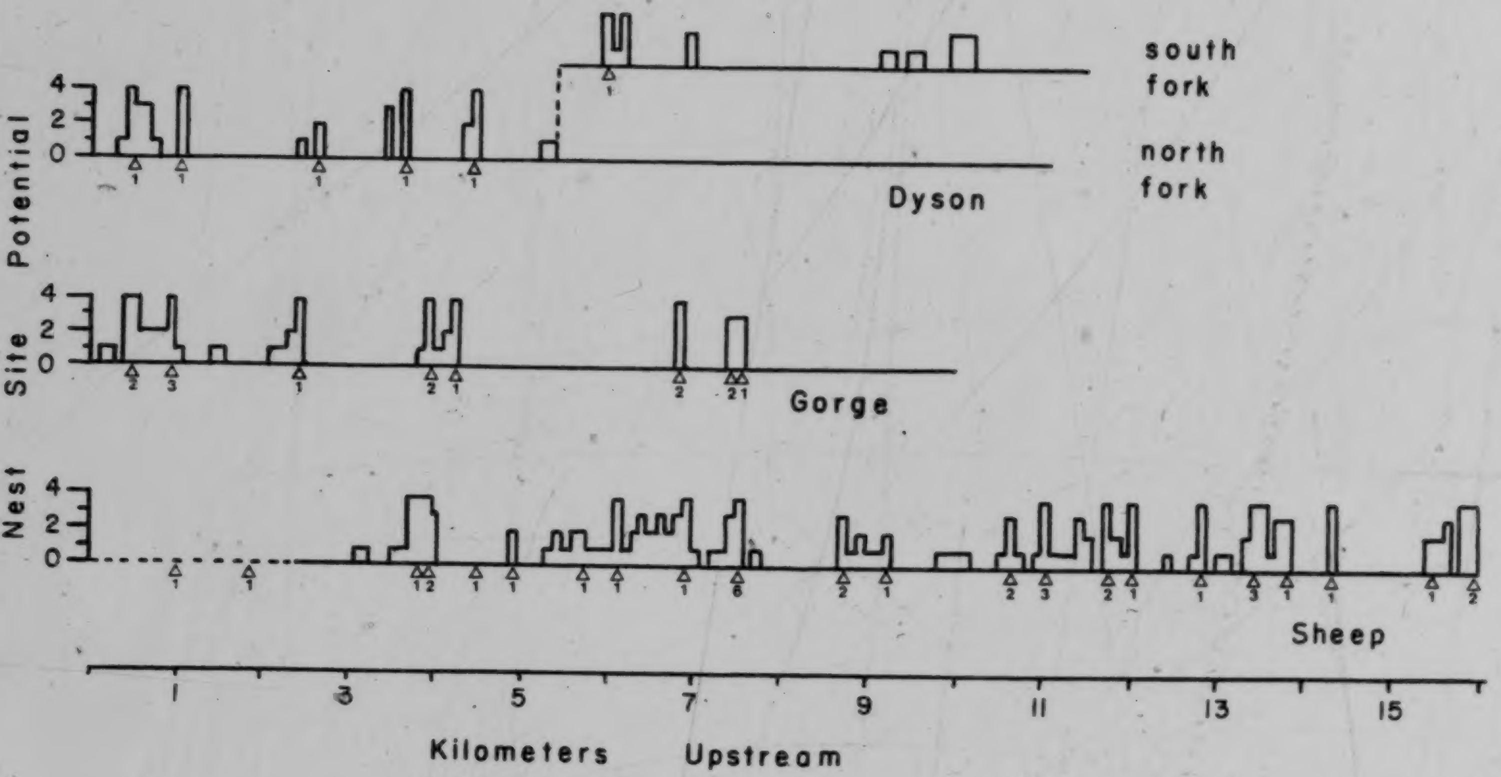

south
fork
north
fork
Dyson
Gorge
Sheep
Stream Morphometry
4
2
0
1
3
5
7
9
11
13
15
Kilometers Upstream

Figure 9. Nest site potential and numbers of nests on the three major streams of the study area. No data for the Sheep River from the mouth of Dyson Creek (km 0) to mouth of Gorge Creek (km 2.5). Classification: 0- essentially no suitable ledges; 1- very few suitable ledges; 2- some suitable ledges; 3- many suitable ledges; 4- abundant suitable ledges. Triangles indicate location and number of nest sites observed.


Potential
Site
Nest
4
2
0
south fork
north fork
Dyson
Gorge
Sheep
1
3
5
7
9
11
13
15
Kilometers Upstream

Population Parameters

Population Size

Censuses were conducted several times during each study season (Table 3) to assess population density immediately before, during, and after the breeding period. Essentially the same lengths of stream were surveyed during each census period, so that the numbers can be directly compared as crude densities. However, during census periods 1 and 8 there was 20 to 50% ice cover on the Sheep River and nearly 100% ice cover on Gorge and Dyson Creeks (except during census period 1, 1976, when less than 25% of each of these creeks was open). The ice cover prevented use of much of these streams by Dippers. The ecological density (Odum 1971:163) was therefore considerably greater than the crude density during these latter censuses. The majority of the individuals in the early spring (census period 1, Table 4) were on the Sheep River, simply because there was little open water on Gorge and Dyson Creeks at that time. Price (1975) found that the distribution of Dippers in winter was highly negatively correlated with ice cover. Sullivan (1973) found that movements of banded Dippers, and hence density on his study areas, were related to developing ice cover.

Dippers arrived in rapid succession on the study area once they began returning from wintering areas (Table 4). All of the Dippers that initiated breeding were present on

Table 3. Periods during which Dippers were censused on Sheep River, Gorge and Dyson Creeks.

Census	Dates of Censuses		Week[1]	Status of Birds
	1975	1976		
1	14-16 April	6-19 April	1-2	Arriving and establishing territory
2	No census	27 April- 17 May	4-6	Pre-breeding
3	10-18 June	7-16 June	10	Breeding
4	No census	10-17 July	14-15	Late to post breeding
5	26 July 2,14-18 Aug.	11-19 Aug.	19	Post-breeding
6	6-21 Sept.	29 Aug.	21-24	Moulting
7	15-22 Oct.	No census	28-29	Dispersing
8	22-24 Feb.	24-27 Feb.	-	Overwintering

[1] Weeks of study were calculated starting from the second week of April each year.

Table 4. Numbers of Dippers observed during censuses on the three main streams of the study area during 1975 and 1976 (see Table 3 for dates of census periods).

Census Period	Breeding Birds						Transients[1]						Juveniles[2]						Unknown					
	Sheep		Gorge		Dyson		Sheep		Gorge		Dyson		Sheep		Gorge		Dyson		Sheep		Gorge		Dyson	
	75	76	75	76	75	76	75	76	75	76	75	76	75	76	75	76	75	76	75	76	75	76	75	76
1. Arrival and territory establishment	0	8	0	1	0	3	0	1	0	1	0	0							16[3]	13	0	1	0	1
2. Pre-breeding	-	15	-	2	8	8	-	2	-	2	2	1							-	8	-	3	-	0
3. Breeding	23	16[4]	10	11	8	8	0	0	0	1	0	1							0	0	0	0	0	0
4. Late and post-breeding	18	16	6	7	4	5	1	0	0	1	0	0	9	10	0	5	12	14	5	1	0	0	1	1
5. Post-breeding	-	13	-	3	-	5	-	0	-	0	-	0	-	16	-	3	-	8	-	6	-	0	-	2
6. Early fall	14	12	7	6	5	4	1	0	0	0	0	0	1	13	1	3	1	4	9	7	8	1	10	13
7. Late fall	15	-	0	-	0	-	1	-	0	-	0	-	3	-	0	-	0	-	19	-	4[5]	-	3[5]	-
8. Winter	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3[6]	6	0	0	0	0

[1] Transients were those banded birds observed on the study area, which did not subsequently breed.

[2] Juveniles, by definition, did not occur until the fourth census.

[3] Only part of Sheep River censused; probably 6 to 10 birds missed.

[4] Does not include birds removed, after nest-building started.

[5] Probably all non-residents.

[6] A partial census.

the study area by mid-May in 1975 and early May in 1976. I found that the number of Dippers that initiated breeding on the study area was relatively constant during the study (45 in 1975, 43 in 1976-Table 5). Price (1975) observed some fluctuation in breeding numbers (40, 44, and 32 over 3 years) in a Colorado Dipper population. Sullivan (1973) also found that there was some fluctuation in breeding numbers over 3 years in Montana (45, 35, and 40). In the Colorado population, low production in one year resulted in a decline in subsequent breeding numbers (Price 1975). It is also quite likely that harsher winters produce greater overwinter mortality, and smaller subsequent breeding populations. However, longer term population studies are necessary to confirm this latter hypothesis.

The breeding population of Dyson Creek was the same size both years. Gorge Creek had one additional Dipper in the breeding population of the second year. One Dipper (0922), which bred on Gorge Creek in 1975, actually bred on the Sheep River between Gorge and Dyson Creeks in 1976 after first attempting to establish a territory on or near his previous territory (Little Boundary Falls, Fig. 19). Consequently, this bird and its mate were considered part of the breeding population of the Sheep River in 1976. The breeding population on the Sheep River declined from 23 in 1975 to 20 in 1976. These totals include the population that initiated breeding each year, that is, before removals in 1976 and did not include the replacement birds.

Table 5. The number of Dippers known to be associated with territories on the main study area (Fig. 2) in 1975, and in 1976 prior to removal of three pairs.

Stream	1975	1976
Sheep	23	20
Gorge	10	11
Dyson	8	8
Bluerock	0	2
Cliff	2	2
Junction	2	0
Total	45	43
No. removed on Sheep		6
No. replacing on Sheep		8
Density (birds/km)	1.22	1.16
Breeding population banded	71.1%	81.4%

Including the latter would bring the breeding population on the Sheep River to 28 and the total on the study area to 51, an increase of three pairs over 1975.

I removed Dippers initiating nesting on two portions of the Sheep River (Fig. 3) in May and early June of 1976. This was done in an attempt to determine whether a non-breeding cohort of Dippers existed along the river as was claimed by Price (1975) for the Colorado population and which he also predicted to be present in other populations. Three breeding territories were established in 1976 in the removal areas (Fig. 3) which had contained four breeding territories in 1975; all three pairs were removed in 1976 and were replaced by three pairs, which were subsequently removed. After the second removals one replacement pair was observed (Terrace Falls territory, Fig. 3). None, some, or all of the seven unbanded replacements may have been among the unbanded Dippers seen earlier on the study area during the censuses (Table 4). One of the replacement Dippers had been banded in 1975 (an adult male no. 0916) but had not been seen in 1976 prior to being removed. This Dipper had not been resident on the study area in 1975, having been banded in the spring but not seen again until the late autumn.

The 1976 pre-breeding census showed that 11 unbanded Dippers were present on the study area (unknown Dippers, Table 4) which did not appear to be mated with known residents. Of the 39 Dippers that subsequently bred on the censused area (Sheep River, Gorge and Dyson Creeks but not Junction, Cliff, and Bluerock Creeks), 17 would have been unbanded at that time. Thus, it was unlikely that many, if any, of the unbanded replacements were on the study area when the initial occupants of these territories began breeding. The implications of a possible surplus to territory establishment are discussed in a later section; in terms of population numbers it was apparent that replacement pairs were not drawn from other territories on the study area at the time of removal and, therefore, there were more Dippers potentially able to establish breeding territories on the study area than actually did so.

Following breeding after the 12th week each year, recently fledged juveniles and transient unbanded Dippers of unknown age appeared on the study area. Numbers recorded in late summer were higher in 1976 than in 1975 (Table 4). This was possibly because production in 1976 was significantly higher than in 1975 (Table 7), even though the removal of breeding pairs resulted in fewer clutches being laid in 1976. Some juveniles apparently remained on the study area into the autumn. In 1975 only three banded juveniles were observed to stay on the study area until the early and late fall censuses (Table 4). In 1976, 14 banded juveniles stayed on the main study area at least until the early fall census (Table 4). A large proportion of the unbanded Dippers of unknown age observed at this time were likely juveniles that had developed sufficiently so as to be indistinguishable in the field from adults; that is they were more than a month post-fledging (Sullivan 1973, this study). A larger proportion of known juveniles existed on the study area in 1976 than in 1975 (Table 4). The reasons for this are not clear, however, several possible explanations, either singly or collectively can be invoked. Jones (1951) showed that benthic fauna may decline to as low as 10% of a former level after a severe flood; if such a drastic decline occurred as a result of the mid-June flood in 1975 (Fig. 4) then it may be that the young moved in search of more productive foraging areas. The increased production in 1976 over 1975 (Table 7) may explain some of the increase in young remaining but not all. The available empty territories in the upper removal area on the Sheep River apparently did not provide additional foraging areas, to hold the juveniles on the study area in greater numbers in 1976. Only five Dippers were observed in that 2.5 km stretch of stream, of which two were known juveniles, one an adult, and the remaining two birds of unknown age. In 1975, the same stretch contained three adults and one bird of unknown age during the comparable early fall census.

Changes in numbers seem to follow similar trends on the individual streams (Table 4). The major difference between the Sheep River population and those on the two tributaries (Gorge and Dyson Creeks) was the later occupancy of the two creeks in the early spring. The breeding Dippers were about 1 week later moving onto Gorge Creek than onto Dyson Creek, as indicated by the later initiation of laying among Dippers on Gorge Creek (Table 8). Precise data on the progress of spring break-up are not available to determine whether the creeks differed in period of opening up, however, I believe Gorge Creek was later from my impressions of relative ice cover on these streams during early spring nest checking.

On the first fall census of 1975 several Dippers that had bred on these tributaries were still present, but by the second fall census they had either moved onto the Sheep River (20%) or migrated. The seven unbanded Dippers of unknown age found on the creeks during the late fall census were unlikely to have bred on the study area as only two unbanded residents had stayed to finish breeding. The movement of the breeding Dippers off the creeks was coincident with the beginning of freeze-up; only a little stream habitat bore ice cover at that time, but it occurred mostly over the shallow edges and shallow pools which were preferred foraging habitat of Dippers. Both Price (1975) and Sullivan (1973) showed that ice cover causes movement of Dippers to more open areas.

Movements of Individuals

Investigations of the nature, timing, and function of the movements responsible for changes in population size and density are fundamental considerations of population ecology. I examined different kinds of movements exhibited by members of the Sheep River population. In particular, I was concerned with migration, large scale movements of birds during territory establishment, and movements related to moult and stream conditions. I shall first consider migration.

Migration of birds is defined as a "regular movement of birds between alternate areas inhabited by them at different times of year, one area being that in which the birds breed and the other being an area better suited to support them at the opposite season" (Thomson 1964). There are numerous references which indicate that cinclids do migrate; concentrations have been reported in wintering areas that are unsuitable for breeding (Pastukhov 1961, Hogstrom 1962, Iygi 1963, King et al. 1973, Pomarnacki 1975), occasional winter sightings of cinclids in areas far from any possible breeding areas (Green 1970, Muelhausen 1970, Sadler and Myres 1976) and documented cases of scattered migratory movements by banded European Dippers (Jost 1969, Andersson and Wester 1975). Despite this, certain populations of cinclids are relatively sedentary (Bent 1948, Robson 1956, Shooter 1970, Sullivan 1973, Salt and Salt 1976). This spectrum of published statements on the nature of migration in the Cinclidae seems to reflect the range of winter conditions in different parts of the breeding range.

A large proportion of the Alberta population migrated from the breeding area. This was shown by the low numbers of Dippers observed on the study area in the winter. The

1975 winter census (Table 4) was an incomplete, preliminary survey; it merely showed that Dippers stayed on the study area during the winter. A portion of the Sheep River from Underground Streams to Junction Creek (Fig. 3) stayed open throughout the winter, in addition to large holes in the ice scattered from Junction Creek to just upstream of Sheep Falls. Dippers were occasionally found at these holes, but were concentrated on the open stretch during both winter censuses. The 1976 winter census revealed one banded resident Dipper. The six other Dippers seen were unbanded and may have included the two unbanded breeding residents from that region. Sullivan (1973) stated that nearly all of the breeding birds remained on the Montana study area in the winter, while Price found that only 20 to 50% of the breeding birds remained on the Boulder study area. Price attributed this difference to amount of ice cover.

There appears, then, to be a gradient in the proportion of a Dipper population that migrates from a breeding area. The proportion depends upon the degree of ice cover on streams in a particular area. It is reasonable to assume that in a mild winter a larger proportion of a population would stay on its breeding area because of the reduced ice cover.

In the early spring, Dippers were extremely mobile in their search for nesting territories. One Dipper in particular (4407), which had been vigorously attempting to establish a territory near the mouth of Gorge Creek, was

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observed to fly 8.5 km upstream on Gorge Creek in 1 day during the second week of April in 1976. It was observed 2 weeks later, 1 km upstream of Gorge Creek on the Sheep River (Fig. 2). Such a distance is considerable when one notes that nearly all Dipper territories were less than 3 km long (Table 26).

Once Dippers have returned to their breeding grounds they carry out all activities within their territories, from which they rarely move. Sullivan (1973) found that 75% of all observations of Dippers away from their breeding territories were during the moult. Price (1975) also found Dippers leaving their breeding territories and apparently moving upstream to areas with more abundant cover during the moulting period. On the Sheep River study area during the early fall censuses, 75% and 85% (1975 and 1976, respectively) of all banded breeding Dippers were still present within their territories. Three of the banded residents, missed during the early census, reappeared on territory during the late fall census in 1975. Therefore, I did not find any large-scale movement away from the territories during the moult. However, Dippers did change their habits as a result of moult, for they were more frequently seen near log jams or seeking cover among rocks during this period.

Dippers were observed away from their territories on a few occasions during periods of high water. At these times the streams were very turbid. One observation was at a shallow lake several hundred meters above the Sheep River; a Dipper was observed foraging in this lake only once during the entire study, even though frequent visits were made to the lake throughout the two study seasons. At the time of the observation the lake was considerably clearer than the Sheep River, which was at its highest level in 1975 (Fig. 4). On a few other occasions, when the main streams were extremely turbid, Dippers were observed foraging in clearer small tributaries or shallow channels of the main stream. Two of these observations were about 100 m within an adjacent pair's territory; such trespass was never observed again during the nesting cycle. Sullivan (1973) also found that 6% of all movements off the nesting territory were related to high water.

Sex Ratio

The sex ratio in breeding populations of birds has been shown to influence their productivity and hence success (Kolman 1960, Willson and Pianka 1963, Verner and Willson 1966, Orians 1969, Jenni and Collier 1972, Holm 1973). Price and Bock (1973) reported polygyny in a Dipper population in Colorado. Price found that productivity was significantly higher among polygynous than monogamous birds, in 2 of the 3 years of his study. Price and Bock (1973) suggest that polygyny may occur frequently in small proportions of breeding populations of Dippers throughout their range. Polygyny has also been reported for Cinclus cinclus (Mork 1975). Unless there is an unbalanced sex ratio among young Dippers, unlikely in a passerine bird (Thomson 1964), or differential loss of the sexes, then a surplus of non-breeding males would result from the polygynous mating system observed by Price (Selander 1965, Zimmerman 1966).

I examined the sex ratio of the population of banded adult Dippers present during censuses (Table 6). The sex of all banded birds was deduced either from observations of nesting behaviour which is sex specific (Bakus 1957, Sullivan 1973, this study) or from measurements taken of body parts at banding (Appendix II).

With the return of banded birds in 1976 it was possible to document the arrival of the sexes; in early spring there were 2.5 males present for every female (Table 6). This suggests that male Dippers return to their territories before females; this is a typical phenomenon among the passerines, in which the male returns first and establishes a territory to which a female is attracted (Hinde 1956, Thomson 1964, Klomp 1972). Even when the mate of the previous year survived, males preceded females onto the breeding grounds. In 1975, a pair (male 0924 and female 0923) held a territory on Dyson Creek. In 1976, the female was found on 6 April along the Sheep River 3 km upstream of the mouth of Gorge Creek. On 13 April, when the first census was made on Dyson Creek, the male was on territory 4

Table 6. Sex ratio of Dipper population observed during censuses on the study area (see Table 3 for dates of census periods).

	Number Observed				Sex Ratio (M/F)	
	1975		1976			
Census Period	Males	Females	Males	Females	1975	1976
Arrival and Territory Establishment	unbanded at this time		10	4	-	2.50
Pre-breeding	few banded		15	13	-	1.15
Breeding	21	20	17	17	1.05	1.00
Late and post-breeding	not conducted		14	15	-	0.93
Post-breeding	12	16	9	11	0.75	0.82
Early fall	15	12	10	12	1.25	0.83
Late fall	8	10	not conducted		0.80	
Winter	unbanded		1	0	-	-

km upstream, but the female, presumed to still be on the Sheep River, was not observed until the prebreeding census of Dyson Creek, at which time the pair were building a nest. Similarly on Gorge Creek, I found the male (0926), of a pair that nested on this stream in 1975, on territory on 14 April, 1976, at a break in the ice cover. The female (0936) was not observed until the second census of Gorge Creek on 13 May. I also observed two males that may have arrived on territory concurrently with their respective mates. Both members of a pair (male 4401 and female 0932) were observed on the same territory (Grab-to-band, Fig. 3) held in 1975, on 7 April, 1976. A female (0931) was found with an unbanded male, probably the unbanded mate from 1975, on its Dyson Creek territory on 13 April.

After the period of arrival the sex ratio was approximately balanced (Table 6). This indicated that neither sex was disproportionately represented. Furthermore, among the 18 banded transient adults observed on the streams during the study, nine were identified as males and nine as females. Thus, the sex ratio among the birds of passage, some of which represented a potential surplus, also appeared to be equal.

Sullivan (1973) implied that Dippers pair for life. During this study three pairs, in which both individuals were banded returned to the same territory where they had bred the previous season. Banded males which returned without mates, acquired new mates. No banded females

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returned which had lost their mates. I saw no evidence of mate exchange among the other marked Dippers.

Natality

More young Dippers fledged in 1976 than in 1975 (Table 7), despite fewer breeding individuals in 1976. A flood in 1975 was the major cause for the difference; it washed away a number of nests and only a few of the pairs that renested were successful.

The timing of breeding varied with location on the streams (Table 8) and between years. There is some indication that nesting is initiated later at higher altitudes and in tributary streams. The uppermost nests on the Sheep River (three in 1975, two in 1976) were initiated later than all nests downstream. There were two exceptions: Panorama Rapids (Fig. 3), where the first egg was laid slightly before 4 July, 1975 (Table 8), was almost certainly a renest; and Joe's Canyon (Fig. 3), where the first egg was laid 20 June, 1976 (Table 8), was a second attempt at territory establishment for male 0922. A nest found at the headwaters of Burns Creek (Fig. 2) was at 2133 m altitude and the first egg was laid in that nest on 20 June, 12 days later than the latest pair on the Sheep River at 1707 m altitude. Sullivan (1973) also recorded later nesting at higher altitudes.

Table 7. Number of young fledged on the study area.

Stream	Number of Fledglings 1975	1976
Sheep	25	22
Gorge	2	13
Dyson	13	14
Cliff	5	5
Bluerock	-	0
Junction	2	-
Total young fledged	47[1]	54
Total adults nesting	45	39
Young/adult	1.04	1.38

[1] This does not include four additional young that would probably have fledged had I not disturbed them.

Table 8. Locations of nests and dates of first egg laid (estimated or observed), 1975 and 1976.

Location		Date of First Egg	
Stream	Kilometer	1975	1976
Sheep	-1.6[1]	--	20 June
	1.5	15 June[2]	27 May
	3.7	4June	20 May[3]
	4.5	1 June	16 May
	5.1	15 May	16 May
	6.2	--	18-23 May
	8.3	10-20 June	11-14 May
	8.7	11 June	--
	9.7	17 May	10-12 May[3]
	11.0	<5 June	1 June
	11.9	13 June	--
	13.1	15-20 June	--
	13.6	--	8 June
Dyson	0.5	4 June	1 June
	2.7	10-15 June	28 May
	3.6	7 June	28 May
	4.5	4 June	24 May
Gorge	0.5	5-15 June	
		1 June	
	0.9	2-4 July[4]	8 June
	2.4	9 June	7 June
	4.0	--[5]	29 May
	6.9	13 June	--
	7.9	--	6 June
Cliff		unknown	5 June
Junction		22 June	--
Burns Creek Falls		--	20 June

[1] 1.6 km downstream of mouth of Gorge Creek. All other kilometer locations are upstream from mouth of Gorge Creek on the Sheep River.

[2] Two nests were occupied within 15 m of each other; the nest recorded was the later one of the two; the other was washed away.

[3] An estimate for a pair removed before clutch laid.

[4] Only nest found here; probably a renest.

[5] No eggs laid.

Later nesting at higher altitudes was not a clear-cut phenomenon within the majority of the study area for two reasons: (1) part of the Sheep River stays open at various points along its course all year long allowing Dippers in those areas to occupy territories sooner than others, or even to remain all winter long (see p. 57), (2) melting of the ice cover is delayed on certain sections of the streams because of the nature and orientation of the banks, for example, in steep, narrow, shaded canyons, the ice thawed much later than in open, more exposed, flatter stretches of the streams. This probably explains the slight lag in reproductive events shown by the two pairs on lower Dyson Creek, and the pairs nesting immediately upstream from the mouth of Gorge Creek on the Sheep River.

In 1976, egg-laying in those territories re-occupied was 1-to-2 weeks earlier than in 1975, probably the result of a 3-to-4 weeks earlier opening of the streams in 1976. Therefore, time of opening of streams appears to have a major influence on timing of breeding in Dippers.

Mortality

There are three consecutive periods in the life of a bird which exhibit differential degrees and types of mortality and are, therefore, generally treated separately (Gibb 1961, von Haartman 1971). The first involves mortality in the nest and occurs between laying and fledging. The second, which includes juvenile mortality, occurs between fledging and arrival of the sexually mature bird on its breeding area. The last period encompasses the adult life-span when annual mortality seems to take a very constant proportion of the population.

Survival through the first period is frequently referred to as "breeding success" of a population or a pair. The breeding success in the population of American Dippers studied compared favourably with that of other populations of cinclids (Table 9). Clutch size and percent of eggs fledged were similar to those reported for other studies; percentage of broods in which at least one young fledged was higher (Table 9).

Juvenile mortality is more difficult to quantify because of the inability to separate dispersal from mortality. In this study I made no attempt to estimate this phase of mortality but rely on that of Price (1975). He estimated 67 and 77% mortality of juveniles, in 2 years, over their first winter. Because Dippers breed as yearlings (Sullivan 1973, Price 1975, this study), all mortality after the first year is of sexually mature individuals. Price observed five and eight 1-year-old Dippers returning to their natal streams over two years, which represented 7 and 12% of the previous year's production. I observed only one returning 1-year-old (0940) which represented only 2% of the 1975 fledglings, and which subsequently bred upstream of the study area. Dispersal and/or mortality may be responsible

Table 9. Comparative breeding success of populations of the genus *Cinclus*.

Mean Clutch Size	% Fledged Based On Eggs	% Fledged Based On Broods	Species And Location	Reference
			C. mexicanus	
4.3	55.8	72.2	Alberta, Canada	This study
4.3	56.5	61.8	Colorado, U.S.A.	Price (1975)
4.1	68.8		Montana, U.S.A.	Sullivan (1973)
4.7	47.4	57.1	Montana, U.S.A.	Bakus (1959a)
			C. cinclus	
5.1			Norway	Andersson and Wester (1975)
3.7[1] 4.3[2]	61.6		Great Britain	Shooter (1970)
3.4[3]		52.5	Great Britain	Hewson (1967)
4.7	50.6	38.6	Czechoslovakia	Balat (1964)
4.1	75.0		Great Britain	Robson (1956)
			C. pallasii	
4.0[4]			Japan	Haneda and Koshira (1967)

[1] Nests above 250 m altitude.

[2] Nests below 250 m altitude.

[3] Abnormally low value likely the result of small, unrepresentative sample size.

[4] Mode.

for the discrepancy between the two studies, although this difference was small.

Adult mortality is easier to determine as these birds return to the territory and nest site previously occupied (Bakus 1957, Sullivan 1973, Price 1975) or within a few km (this study). The overwinter mortality was 53% for the Dipper population on the Alberta study area (Table 10). A high percentage survived the winter and returned. Two Dippers disappeared during each breeding season, abandoning their mates and nests on the Sheep River study area and were presumed to have died. This would mean a breeding season mortality of approximately 5%, and an estimated annual adult mortality of 56% (Table 10). Price (1975) found that annual adult mortality ranged from 47.5 to 61.4% for 2 years of his study in Colorado. Robson (1956) recorded an annual mortality of 64.4% for European Dippers, although he included post-fledging young and adults in his estimates, which are, therefore, not strictly comparable. Juvenile mortality was shown to be quite high among populations of the American Dipper, so that Robson's estimate probably overestimates adult mortality. Annual adult mortality among passerines was estimated at 40 to 60% by Lack (1954) and 40 to 70% by Farner (1955). Price (1975) stated that annual adult mortality of Dippers is therefore similar to what one would expect of this passerine. My data support his conclusion.

Table 10. Maximum annual mortality among banded adult Dippers obtaining breeding territories on the study area.

	Sheep	Dyson	Gorge	Study Area
Banded in 1975	19	5	8	32
Returned in 1976 (%)	6 (31.8)	4 (80)	4 (50)	14 (43.8)
Overwinter mortality (%)	13 (68.2)	1 (20)	3 (38)	17 (53.1)
Oversummer mortality (%)			1 (12)	1 (3.1)
Annual mortality (%)				18 (56.2)

Documented cases of Dipper mortality are rare in the literature. It is therefore difficult to ascribe the apparent annual mortality to particular factors. Predation has been recorded only once; Johnson (1953) reported finding a juvenile Dipper in the stomach of a large brook trout (*Salvelinus fontinalis*). Steiger (1940), without supporting evidence, stated that Dippers were regularly preyed upon by a series of mammals. Sullivan (1973) discounted Steiger's undocumented statements and suggested that avian predators may periodically catch Dippers, although all attempts which he observed by *Accipiter* spp. were unsuccessful. Dippers may avoid avian predators by flattening on the surface of the water and remaining motionless (Sullivan 1973).

I observed several unsuccessful attempts by *Accipiter* spp. to catch Dippers of varying ages; some of these attempts were upon moulting adults. In 1975, my assistant, C. Kullman, witnessed a Cooper's Hawk (*Accipiter cooperi*) kill a fledgling, 6 days out of the nest. One of the parents, the adult male (0920), observed the hawk and prevented it from attacking one fledgling by flying towards this fledgling and chattering; while the adult's attention was so diverted, the hawk quickly flew about 20 m downstream and caught the other, unsuspecting fledgling. Mink (*Mustela vison*) were observed on the study area and may have constituted a threat to birds along vegetated streams; no nest predation was recorded, so mink and other mammals were unlikely to have been important predators.

Other reported causes of mortality are starvation (Price 1975), disease (nestlings observed by Sullivan, 1973), and flooding (Robson 1956- European Dipper, this study). The highest percent mortality of adults and likely of juveniles occurred between breeding seasons (this study), suggesting that the rigours of migration and the reduced available habitat during the winter as a result of streams being covered with ice, take their toll of Dippers.

Dispersion

The spatial distribution of members of a population at one point in time is termed dispersion - the result of movements of animals in response to environmental and social parameters (Brown and Orians 1970). This response may result in one of three distributions: random, clumped, or regular. The dispersion of birds, during the breeding season, must be related to nest site requirements and, ultimately, to nutritional requirements of the young, particularly for birds possessing type A territory (Nice 1937).

Price (1975) examined the distribution of Dippers in relation to environmental variables and social behaviour. Distribution of Dippers was positively correlated with food for much of the year, although the correlation was much weaker on one study stream than the other and weaker during the breeding season than during the winter. In addition, he found that distribution, during the breeding season and occasionally other periods, was positively correlated with units of stream having high nest site availability and high quality of nest sites.

Price (1975) examined dispersion of breeding birds particularly the aspect of territory size and factors affecting that size. I also examined dispersion of breeding territories but defer the discussion of this analysis to the section on Territory Distribution and Function (below).

I examined distribution of Dippers in relation to each other during pre- and late-to-post-breeding censuses, because it added another dimension not treated in Price's analysis of Dipper dispersion relative to environmental variables.

Given that the Dipper is generally an aggressive bird, with a complex repertoire of agonistic behaviour (Sullivan 1973), it is of interest to note that their dispersion during most censuses was significantly clumped (Figs. 10, 11). Under what circumstances did Dippers tolerate the presence of another Dipper within a distance at which these mobile birds should have been aware of each other?

During certain of the censuses (Figs. 10, 11) it was obvious that the Dippers were clumped merely because of breeding relationships (Table 11). This is not surprising for a monogamous species possessing a Type A territory (Nice 1937). Some territories had already been established in early April when Dippers were moving through the study area.

Figure 10. Frequency histograms of nearest neighbour distances between Dippers, during population censuses in 1975 and winter 1976. Observed distribution (solid lines) were compared with a Poisson distribution (dotted lines). Nearest neighbour distances are multiples of 200 m. A -Sheep River, 15 April. B -Entire study area, 26 July- 18 August; $p<0.001$. C -Entire study area, 2-21 September; $0.2>p>0.1$. D -Entire study area, 15-21 October; $p<0.001$. E -Sheep River, 24-26 February.

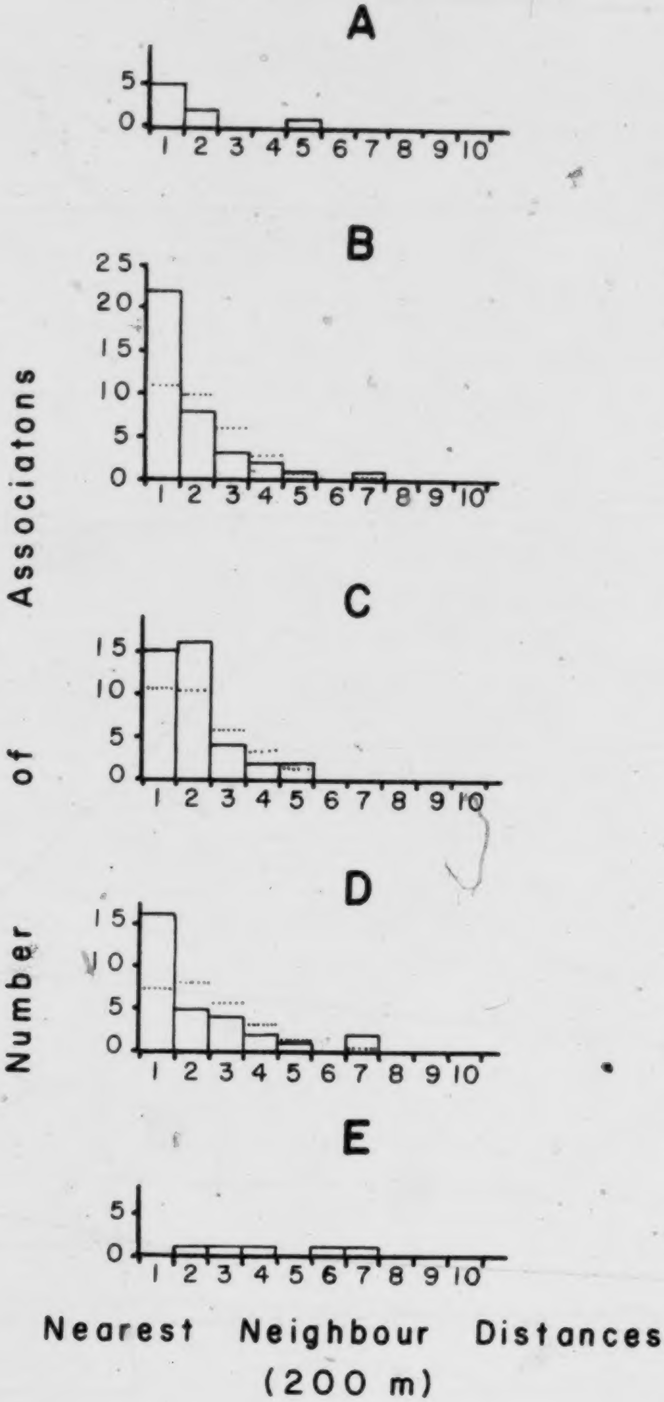
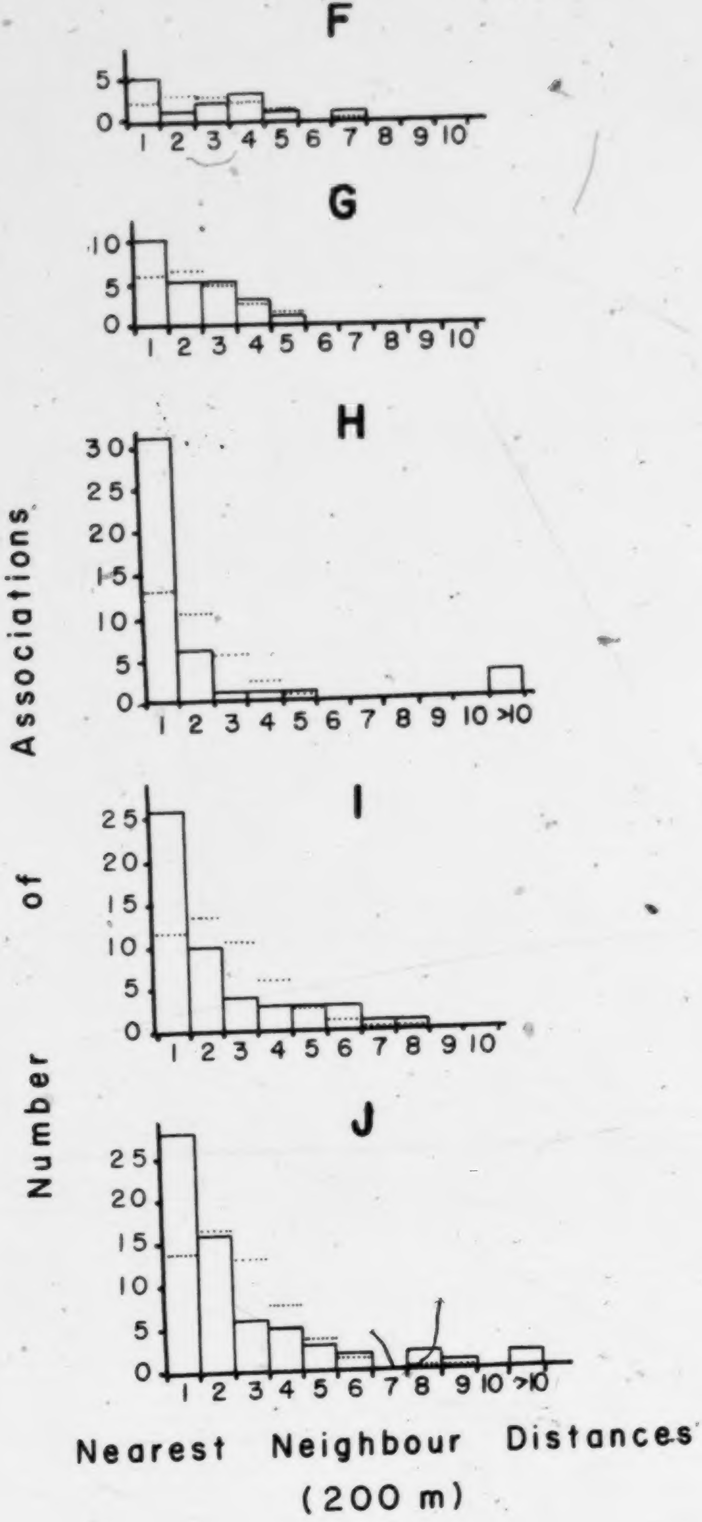

A
B
C
D
E
Number of Associatons
0
5
10
15
20
25
1 2 3 4 5 6 7 8 9 10
Nearest Neighbour Distances
(200 m)

Figure 11. Frequency histograms of nearest neighbour distances between Dippers, during population censuses in 1976. Observed distributions (solid lines) were compared with a Poisson distribution (dotted lines). Nearest neighbour distances are multiples of 200 m. F - Sheep River, 6-7 April; 0.2>p>0.1. G -Sheep River, 27-29 April; 0.7>p>0.5. H -Entire study area, 8-16 July; p<0.001. I -Entire study area, 11-20 August; p<0.001. J -Entire study area, 29 August- 7 September; p<0.001.


F
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1 2 3 4 5 6 7 8 9 10
G
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1 2 3 4 5 6 7 8 9 10
H
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25
30
1 2 3 4 5 6 7 8 9 10 >10
I
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1 2 3 4 5 6 7 8 9 10
J
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15
20
25
1 2 3 4 5 6 7 8 9 10 >10
Number of Associations
Nearest Neighbour Distances
(200 m)

Table 11 Dippers associated within 200 m during censuses.

Census Period[1]	Breeding Pair	Adult and Offspring	Siblings	Moult[2]	Juveniles[3]	Others
B	4	13	1	-	-	4
D	-	-	-	-	-	16
H	8	17	5	-	-	2
I	2	2	2	9	5	6
J	2	2	1	2	7	14

[1] See Figs. 10, 11 letter reference and date of census period.
[2] One member of "pair" was moulting and flew poorly.
[3] Association between at least two juveniles.

Also, territories may be persistent into the early fall, for, as shown earlier (p. 55), many breeding Dippers remained on their territories well past the fledging of the young.

During the late summer to late fall, Dippers were observed to be clumped in distribution (Figs. 10, 11). I discovered upon examining the nature of these associations that relatively few were between mates, adults and offspring, or siblings, and that during the August 1976 census 70% of the associations involved either one moulting individual and another bird or at least two juveniles, while 43% of the associations observed during September 1976 were of such types.

Moulting individuals might be expected to be more tolerant of other individuals because of their reduced ability to fly and, therefore, their reduced ability to defend an area. On one occasion I observed a moulting adult (0909), tolerate an unbanded intruder, which passed it extremely closely while both were foraging near the former's nest. At one time the resident assumed a horizontal, cryptic posture similar to "Flattening" (Sullivan 1973:27) and kept quite still upon the first appearance of the wandering intruder. On two occasions 0909 did attack unbanded juveniles that approached within less than 1 m, but in each case there was no subsequent chasing and the juveniles simply maintained a distance of at least 5 m during foraging from then on. Therefore, moulting residents were more likely to tolerate other Dippers closer than those birds capable of flying better. The fact that intruders should be seen so frequently near moulting residents implies that both may be responding to an area of perhaps abundant, easily obtainable food or secure roosting sites. The stream environment exhibited considerable heterogeneity and the birds may have responded to "clumps" of favourable habitat.

A number of the groups observed during the censuses when Dippers were significantly clumped were associations of juveniles. During the censuses and occasional observations during the fall, I observed several chases involving two or more juveniles. It is unclear what the function of such associations may be, but they were a distinct feature of this period. Price (1975) provided evidence that dispersal may occur during the 3-month post-fledging period. A mechanism for dispersal which may function through aggression has been suggested for some populations of field voles, although results were ambiguous (Myers and Krebs 1971). Although comparable evidence among birds is also not conclusive, and tests of the hypothesis that agonistic behaviour increases dispersal are few in number (King 1973), there remains the possibility that agonistic behaviour provides a mechanism for dispersal. In addition, it seems unlikely that the agonistic interactions between juveniles were operating simply as spacing mechanisms because their distribution on the stream was clumped. Also, occasionally a group of two or more banded juveniles were observed travelling together, which did not suggest a spacing mechanism in operation.

During October 1975, moulting individuals or associations of known juveniles could not be invoked to explain the clumped distribution (Table 11). However, all of the Dippers observed in close associations were found between Bluerock Creek and Underground Streams, on the Sheep River (Fig. 3). Although there was some ice on the small tributaries, most of the streams were accessible for foraging. Upstream of the study area on the Sheep River, the stream flow had gone underground. Therefore, from a point 2.5 km upstream of the Underground Streams (Fig. 3), to a point about 4 km further upstream there was no suitable foraging habitat for the Dippers. This lack of good foraging habitat upstream may have caused the observed clumping. However, this does not seem entirely likely, because some of the birds observed in this region were residents from downstream. Another point is that there was no indication of a clumping of food in that area (at least during the last sampling period, Fig. 16) or roosting habitat (similar to nesting habitat, Fig. 9) which might explain why the Dippers were only found in that 4.5 km region. On the winter census (February 1976) I found six of the seven Dippers observed on the Sheep River within that region. It may be that the Dippers were attempting to procure a winter territory on that part of the Sheep River that stays open throughout the winter.

The lack of clumping during the September 1975 census is curious. It may be that the Dippers were well dispersed because many were moving away from territories at this time, possibly as a precursor to migration or while moving to the region in which they were clumped during the late fall census. The number of Dippers fledged was lower that year so that interactions between juveniles would have been fewer. The census was several days later than the early fall census in 1976 which meant fewer adults were still undergoing moult. These factors might account for the reduced clumping of Dippers with respect to each other, at this time.

Dispersal

The movement of a juvenile bird from its natal area to its first breeding area is called dispersal (Berndt and Sternberg 1968). Berndt and Sternberg also included under this term the movements of adult birds from one breeding area to another, although, these are generally less frequent. The mechanisms responsible for dispersal are generally attributed to innate processes, whereas dispersion (the actual distributions of individuals in space) is related to external processes (Berndt and Sternberg 1968) that may be abiotic or social in nature. The distance and orientation of dispersal movements are dependent upon: habitat selection for breeding by the birds, the availability and distribution of suitable habitat, and mobility of the bird which determines the distance that is travelled in searches for breeding habitat.

Relatively few (7 to 12% in Colorado, Price 1975; 2%, this study) Dippers return to their natal area to breed after their first winter. Dispersal is, therefore, usually some distance away from the natal area. Price estimated the proportion of juveniles dispersing away from the Colorado study area as 80%, by dividing the number of foreign recruiting individuals each year (assumed to be first-year birds) by the total number of recruiting individuals. Observations of marked juveniles indicated that some arrived at their future breeding sites during their post-fledging movements and before migration, while others had not settled after 11 months (Price 1975).

Only one banded male juvenile returned to the Sheep River study area in 1976; it was later observed feeding nestlings on Burns Creek about 8 km upstream of the main study area (Fig. 2). Therefore, none of the 48 banded fledglings of 1975 returned to breed on the study area; among those surviving the winter, all dispersed widely.

Price (1975) concluded that much of the dispersal occurred during the 3-month period of post-fledging. In examining these movements further, Price discovered that they were not random; of those birds that he could follow, approximately 28% moved downstream during this period and the remainder moved upstream or changed drainages (which probably occurred after upstream movements, as shown by Jost (1969) for European Dippers).

Of 103 fledglings that I banded in 1975 and 1976, 63 were observed during the post-fledging period. The 40, that were not observed subsequently, were assumed to have moved in undetermined directions out of the census area after fledging. Of the 63 observed during post-fledging, only 23 were observed to move more than 1 km away from their nests; 17 moved upstream, while 6 (26%) moved downstream. There appeared to be no difference in post-fledging movements between the Colorado and southern Alberta populations. If dispersal were to occur mainly during the 3-month post-fledging period as Price found, then one would expect a higher proportion of juveniles to move downstream in the Alberta study area because breeding habitat continued downstream for several km unlike the Colorado study area, where there was no Dipper breeding habitat downstream. A larger proportion of Dippers in the Sheep River study area were forced to migrate than in other populations studied (Bakus 1957, Sullivan 1973, Price 1975). Dispersal may occur during migration and with more birds migrating, more may disperse away from their natal areas. Further study is needed to clarify the process of dispersal in Dippers. However, there are some indications that the process is one which may vary according to the population investigated, in contrast to populations of more sedentary species (Halliburton and Mewaldt 1976).

Nest Site Distribution and Selection

A total of 74 nest sites were discovered during the study. The occurrence of nest sites tended to be clumped in areas of abundant suitable ledges. Of the 74 discovered, 62 were found on the main study area (Fig. 9). The Sheep River had an abundance of sites, particularly along certain stretches while both Gorge and Dyson Creeks had relatively fewer sites available. Therefore, nest sites appeared to be potentially limiting on the Creeks, but not on the main river.

I attempted to determine why several nest sites were not being used on the Sheep River, by examining features that might be related to nest site selection such as: security from predators, protection against adverse weather conditions, endurance of nest site throughout the breeding season and security from high water. The first three of these factors are important factors in the success of solitary-nesting bird species in general (Kendeigh 1942).

Muir (1894) claimed that Dipper nests were nearly always placed where they were kept wet by spray, and that this kept the nest material (mosses) "alive and growing" and in good condition throughout the breeding season. Hann (1950) found that not even a majority of the nests observed by him were kept wet. In the present study, slightly more than half of all nests used were kept slightly to extremely wet. There was no apparent advantage to having a wet nest, both dry and wet nests being approximately equally represented among the unsuccessful nest sites (excluding the flooded nests). Therefore, it is unlikely that wetting of the nest directly played a major part in nest site selection.

Dipper nest sites frequently exhibited attributes of: high noise level nearby, high inaccessibility, low conspicuousness, high stability of rock-face, large overhang and directly over water (Fig. 12). Without a good estimate of all the ledges on the cliff faces possessing various levels of these attributes, it is impossible to quantitatively compare the number of suitable ledges available with those used. A more meaningful comparison is probably that between those sites that were used during the present study and those that were not used. The former group included all sites at which Dippers bred, while the latter group consisted of sites in which residents built additional nests (partial or complete) before breeding or after the floods, and sites which were not even visited during the study. The used sites were significantly noisier, less accessible, on stabler substrate, and closer to fast water than the sites that were not used (Table 12). I found no difference between the two types of nest site in degree of conspicuousness, size of overhang, whether over water or not, nor in the depth of water below the nest. Therefore, in general, a noisy, inaccessible, stable site which is near fast water or a falls was preferred over others that were less so.

Figure 12. Characteristics of all nest sites observed on the study area. See Table 1 for details of the characteristics.

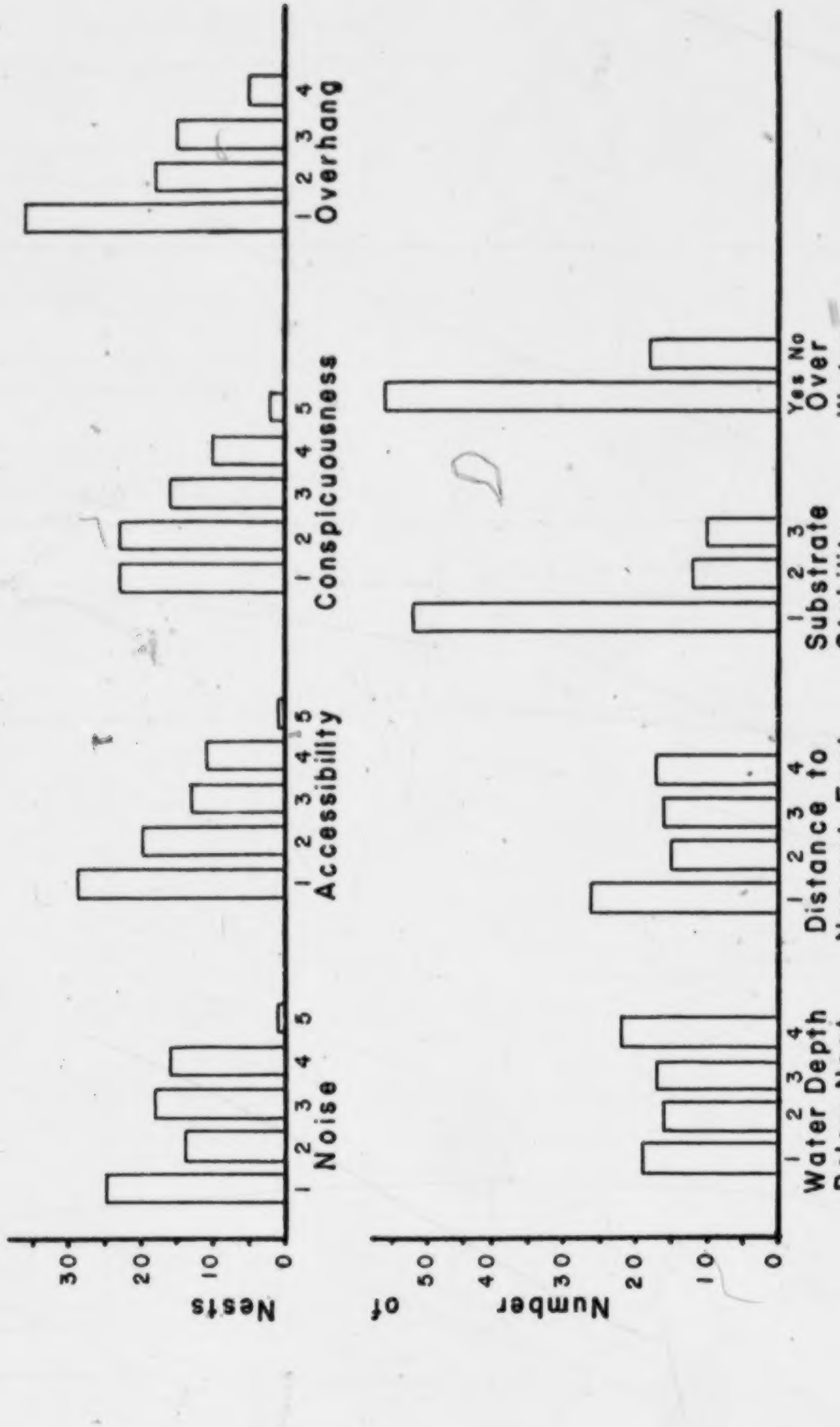
Number of Nests
0
10
20
30
Noise
1
2
3
4
5
Accessibility
1
2
3
4
5
Conspicuousness
1
2
3
4
5
Overhang
1
2
3
4
0
10
20
30
40
50
Water Depth Below Nest
1
2
3
4
Distance to Nearest Fast Water
1
2
3
4
Substrate Stability
1
2
3
Over Water
Yes
No

Table 12. Comparison of features at used nest sites with unused nest sites.

Feature	Category[1]	Used	Unused	X^2	Probability
Noise	1	20	4	9.3	$p<0.05$
	2	10	4		
	3	10	5		
	4+5	6	10		
Accessibility	1	27	1	19.1	$p<0.001$
	2	7	10		
	3+4+5	12	12		
Conspicuousness	1	19	4	4.8	$p>0.1$
	2	15	8		
	3+4+5	12	11		
Overhang	1	27	8	4.1	$p>0.1$
	2	10	6		
	3+4	9	9		
Substrate Stability	1	39	10	12.7	$p<0.005$
	2+3	7	13		
Directly Over Water	Yes	33	18	0.3	$p>0.5$
	No	13	5		
Water Depth Below Nest	1	15	3	3.3	$p>0.25$
	2	9	5		
	3	10	6		
	4	12	9		
Distance to Nearest Past Water	1	22	4	6.2	$p<0.05$
	2+3	15	11		
	4	9	8		

[1] Categories were lumped where necessary to meet minimum cell size assumptions of X^2 test (Siegel 1956).

The locations of nest sites in my study area were generally similar to natural nest sites reported from other areas (Table 13). No nest sites were found in trees or in woody debris in the Sheep River study area. Two nests were found in the rather unusual location of a dirt bank above the stream; one of the nests was on the edge of a grassy overhang, while the other was underneath such an overhang. A number of nests on bridges and dams are reported (Bakus 1957, Sullivan 1973, Price 1975). In addition, nests of Dippers have been found in a culvert (Sullivan 1973), on a house (Sullivan 1966), and on a wooden flume (Goodge 1959). In the Sheep River study area there were no nests located on the few bridges present, although one Dipper did nest beneath an old weir on Junction Creek. Therefore, Dippers nested in generally typical, natural nest sites during this study.

I attempted to determine the effect of an abundance of nest sites on breeding numbers and distribution of Dippers. To do this I created artificial nest sites on Gorge and Dyson Creeks where a dearth of nest sites prevailed. Price (1975) put out several nest boxes, similar to those successfully used by Jost (1970) for European Dippers, but was not successful in attracting birds; only one of 10 nest boxes was used during the second summer after installation. I chiseled ledges out of the rock faces over the water and provided an overhang, which I had hoped would be similar to a "natural" nest site and thus acceptable. None of the 11

Table 13. Comparison of nest sites of American Dippers on natural substrates reported in the literature[1] with those on the Sheep River study area and those reported on nest record cards in Alberta and British Columbia.

Location of Nest Site	Literature No.	Literature %	Sheep River No.	Sheep River %	Nest Cards No.	Nest Cards %
Cliff ledge	43	62.4	54	73.0	15	68.2
Waterfall	8	11.7	17	23.0	6	27.3
Midstream boulder	11	15.9	1	1.3	1	4.5
Roots	5	7.2	0	0	0	0
Stump	1	1.4	0	0	0	0
Tree	1	1.4	0	0	0	0
Overhanging dirt bank	0	0	2	2.7	0	0
TOTAL	69		74		22	

[1] adapted from Sullivan (1973). Data compiled from: Bryant and Bryant 1915, Skinner 1922, Rishel 1925, Cordier 1927, Quaintance 1935, Johnston 1943, Cooper (in Bent 1948), Rathbun (in Bent 1948), Saunders (in Bent 1948), Bailiff (in Racey 1948), Hann 1950, Bakus 1959a, Sullivan 1973.

nest sites created on Dyson Creek was used in 1976, while two of the 11 nest sites created on Gorge Creek were used. Of the latter sites, one was used only for initiating a nest; the pair began to build a nest but got no farther than filling all the tiny crevices with bits of moss and then moved to a more inaccessible and less conspicuous nest site about 8 m upstream. The other artificial site used (G-12) was just over 1 km upstream of the Gorge Trail nest site (Fig. 19). The pair built a complete nest after removing the nest I had placed in the site. One egg was laid in this nest but the following day the egg was found in the water below the nest and the nest cup had been removed, apparently by the adults.

The range of values for the features of the artificial nest sites (Fig. 13) were similar to those of all nest sites found. Artificial sites were generally no different than used sites in the depth of water below the nest, the substrate stability, nor the degree of overhang above the site (Table 14). Artificial sites were more frequently directly over the water than the used sites, so in this category they were of higher quality. However, generally the used sites were on noisier parts of the stream, less accessible, less conspicuous and closer to fast water than the artificial sites (Table 14). Therefore, in general, artificial sites were not as attractive as the natural sites. This may explain the small amount of use made of the artificial sites. In addition, the return of at least one

Figure 13. Characteristics of artificial nest sites created for Dippers on Gorge and Dyson Creeks. See Table 1 for details of the characteristics.

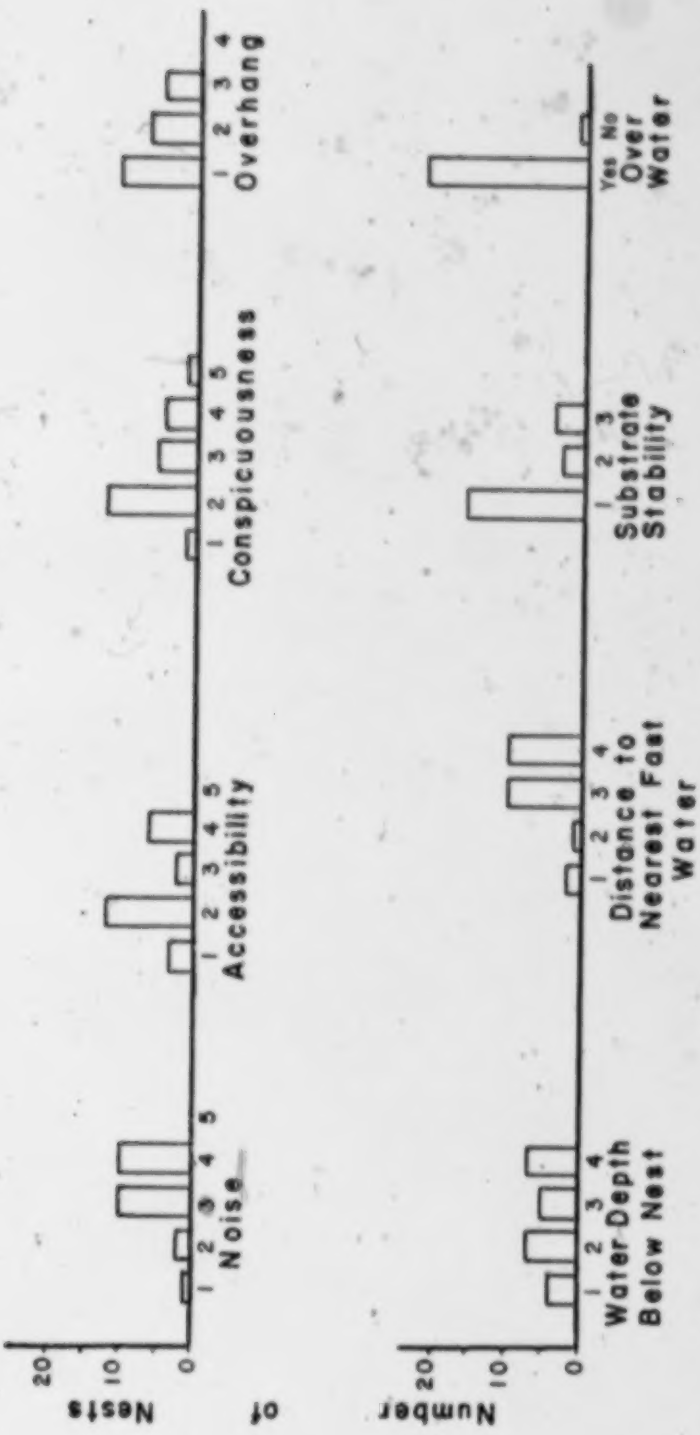
Number of Nests
0
10
20
1 2 3 4 5
Noise
1 2 3 4 5
Accessibility
1 2 3 4 5
Conspicuousness
1 2 3 4
Overhang
1 2 3 4
Water Depth Below Nest
1 2 3 4
Distance to Nearest Fast Water
1 2 3
Substrate Stability
Yes No
Over Water

Table 14. Comparison of features at used sites with artificial sites.

Feature	Category[1]	Used	Artif.	X^2	Probability
Noise	1+2	30	3	17.3	$p<0.001$
	3	10	10		
	4+5	6	10		
Accessibility	1	27	3	15.3	$p<0.001$
	2	7	12		
	3+4+5	12	8		
Conspicuousness	1	19	1	10.1	$p<0.01$
	2	15	12		
	3+4+5	12	10		
Overhang	1	27	11	0.8	$p>0.5$
	2	10	7		
	3+4	9	5		
Substrate Stability	1	39	16	2.2	$p>0.1$
	2+3	7	7		
Directly Over Water	Yes	33	22	5.4	$p<0.025$
	No	13	1		
Water Depth Below Nest	1	15	4	2.1	$p>0.1$
	2	9	7		
	3	10	5		
	4	12	7		
Distance to Nearest Fast Water	1+2	31	3	18.5	$p<0.001$
	3	6	10		
	4	9	10		

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[1] Categories were lumped where necessary to meet minimum cell size assumptions of X^2 test (Siegel 1956).

member of each of four pairs resident in 1975, to the same territories, probably accounted for some of the low use of the artificial sites.

Nest material did not appear to be a cue attracting Dippers to a nest site (Table 15), despite the fact that the only artificial nest sites used were provided with nests. There was no apparent preference for sites with nest material. Thus, the permanent features of the site must attract the Dippers, and not the presence of an old nest in the site, indicating no predation, no flooding, and stability of the site.

After examining the features involved in selection, I investigated nest sites in terms of breeding success. There were several causes of failure of clutches (Table 16). The security or success of a site, may change from one year to the next, independent of the birds using it, because of periodic high water. Flooding and probably some of the unexplained failures were related to the quality of the nest site. Although flooding was responsible for the failure of a number of nest sites, in several cases the adults renested and successfully raised a brood. All renests were started very shortly after the flooding and while the water was still quite high (in 1975) so that the subsequent sites were safer from high water than the original. However, other than in height, all renests were rated lower in quality than the original, in that they were usually more accessible and more conspicuous. Only two renests were in the same

Table 15. Nest sites used in 1975 and in 1976 relative to presence or absence of old nest materials.

	Nest Materials	
	Present	Absent
Avoided	22(10)[1]	21(11)
Accepted	10 (2)	19
Banded Returnees	5	3
New Birds	2	9
Unknown (New or Returning)	1	7

[1] Numbers in brackets are number of artificial sites included in the sample.

Table 16. Loss of Dipper clutches initiated in nests on the study area.

Cause of loss	Number of clutches lost 1975	 1976	 Total
Flooding	8	2	10
Abandoned	2	1	3
Unknown	5	3	8
Eggs froze	1	0	1
Human interference	1	0	1

location as the flooded nest, however eggs were not laid during either nesting attempt by one pair.

The other causes of nest loss showed that certain sites were unsuccessful both years, even though the occupants changed. Other nest sites were successful locations one year and unsuccessful the next. There were cases of a change in the occupants between years and cases of returning pairs that accompanied these changes in site success. There did not appear to be any consistent trend in causes of nest failure.

Sullivan (1973) reported 17 losses out of 79 active nests. Six losses were caused by human activity, two by rising water, three by terrestrial predators, one by intraspecific aggression, and five unknown causes. These losses were over 4 years of study. Price (1975) reported 33 losses of which eight were caused by death of an adult or abandonment by adults, seven were the result of flooding, four of nest destruction (probably three by humans), three of possible genetic damage, one of starvation or disease, one of intraspecific aggression, and seven of unknown causes. In comparison with these other studies, the Alberta population suffered considerably more from high water conditions, and much less, if any at all, from human activity (excluding one nest loss caused by myself).

Floods similar to that occurring in 1975 occur occasionally. Between 1950 and 1963, there were 3 major floods recorded, in 3 different years during the time of breeding by Dippers, in 7 years for which records were kept (unpub. Reports of R. B. Miller Biol. Stn.).

Considering the drastic effect that floods have had on nesting success it is surprising that there has not been selection for nesting in safer locations. Dippers have a long nesting period (about 45 days from start of laying to fledging) which would tend to make their presence conspicuous to predators, as well as increase the period during which they would be susceptible to nest predation. Other birds which nested on the cliff faces of the streams (Townsend's Solitaire _Myadestes townsendi_, and Western Flycatcher) more frequently nested in more accessible locations but their nesting periods were much shorter, and therefore, on a time basis alone, they were less susceptible to predation. In contrast to Dippers, these latter species were often observed to nest on loose shale ledges, which are far more abundant than firm rock ledges; several nest losses were recorded as a result of rocks falling onto these nests. It is interesting to speculate that perhaps Dippers have avoided the more abundant potential nest sites on loose rock faces for two reasons: these sites have a higher potential for damage to the nests from falling rocks, and they are frequently more accessible to mammalian predators. The long nesting period of the Dippers would make such locations doubly hazardous.

Nest site use has been shown to depend upon selection in the Sheep River area. There are three other factors that appear to be involved: nest site fidelity, timing of occupation of a territory for a nest, and the extent of established territories. I defer discussion of this last point to the next section. Nest sites are frequently reused by the same pair of Dippers (Sullivan 1973, Price 1975). Sullivan found that males always returned to the same site even if they lost their mates, while females would move to a new mate's territory if they lost their original mate.

I observed two males to change nest sites: male 0904 moved to a site on the Sheep River in 1976, 5 km from the site on Gorge Creek used in 1975. Male 0922 also moved to the Sheep River in 1976, 4 km from the 1975 site on Gorge Creek. Male 0922 had lost its mate in 1975, while 0904 probably had lost its mate over winter. The former shifted territories as a result of the timing of its return to its 1975 nesting territory. This male did not arrive on its previous nesting territory until at least 2 weeks after it had been occupied by a pair of newly banded birds; this late arrival was in spite of its presence on the Sheep River (near where it eventually bred) very early in 1976 (7 April census).

Timing and extent of territory seems to have governed the use of two nest sites on the upper Sheep River, which were used in 1975 but not in 1976. In 1975, the pairs for Triumvirate and Underground Streams nest sites established territories at the same time as one or both of their adjacent neighbours. In early April 1976, a territory encompassing the 1975 Triumvirate territory and most of the adjacent downstream Sungalashee territory had already been established by an overwintering banded male (0998) and an unbanded female. This effectively excluded new pairs from establishing territories. In 1975, because the two nest sites had been claimed at about the same time (and a couple weeks later than an adjacent upstream territory) both nests were used. Similarly, the territories upstream and downstream of the Underground Streams nest site were established at about the same time and encroached considerably on the portion of stream included in the 1975 Sungalashee territory. The territory upstream of Underground Streams nest site extended at least 500 m into the 1975 Underground Streams territory. The result was that the Underground Streams nest was vacant in 1976.

Sunquist (1976) reported that *C. pallasii* consistently placed their nests in the upstream half of their territories, despite the availability of apparently suitable ledges in the downstream halves of territories. No discussion of nest placement in American Dipper territories has been published. The Dippers in the Sheep River study area showed no preference for upstream or downstream halves of a territory (10 nests in downstream and 7 nests in upstream halves). The only consistent feature about nest placement appeared to be the provision of some degree of a buffer zone; nests ranged from a minimum of 0.2 km to a maximum of 0.75 km away from the nearest territory boundary.

The behaviour of Dippers in nest site selection and in establishment of territories largely determined which ledges on the streams were occupied. Therefore, the effect of social behaviour among Dippers was quite important and it is the implications of this behaviour that I examine in the final section.

Food Availability and Use

The biomass of benthic invertebrates was chosen as a comparative index of available food (standing crop) in different parts of the streams within the study area (Figs. 14-16). The values obtained varied considerably from one sampling site to the next in each sampling period, indicating an uneven distribution of the food resource over the study area in 1976. This is not surprising in view of the variable stream morphometry (Fig. 8) known to affect the amount of biomass that can be supported per unit area of stream bottom (Hynes 1970).

The total biomass per unit area was compared among streams and among sampling times with only a few instances of significant differences recorded (Table 17). The samples obtained from the Sheep River in June weighed less than samples obtained from the Sheep River, Gorge Creek, and Dyson Creek in July and the Sheep River in May (Table 17). Therefore, the highest standing crop of invertebrates was on the entire study area in July, followed by the Sheep River in May. Within the study area the lowest level of benthic biomass was found in June on the Sheep River. The biomass samples from Gorge and Dyson Creeks in June were of an intermediate level.

Price (1975) found that standing biomass in mid-summer (July) was significantly lower than at other periods of the year (April, February, December). I sampled only during the breeding season so that I cannot determine whether a decline

Figure 14. Dry weight of stream bottom samples obtained between 4 and 7 of May, 1976, from the Sheep River. Weights of four samples/station have been doubled to give values that can be compared with eight samples/station obtained during later sampling periods (Figs. 15, 16). Asterisk indicates those stations used for comparison with later sampling periods. Forage ratios (Table 21) were calculated from data recorded at station 14. The blank portions of the figure represent the weight of Ephemeroptera, the close stippling represents Plecoptera, the vertical lines represent the Trichoptera, and the large dots represent other taxa. The increasing numbers are stations increasingly further upstream from the mouth of Gorge Creek.

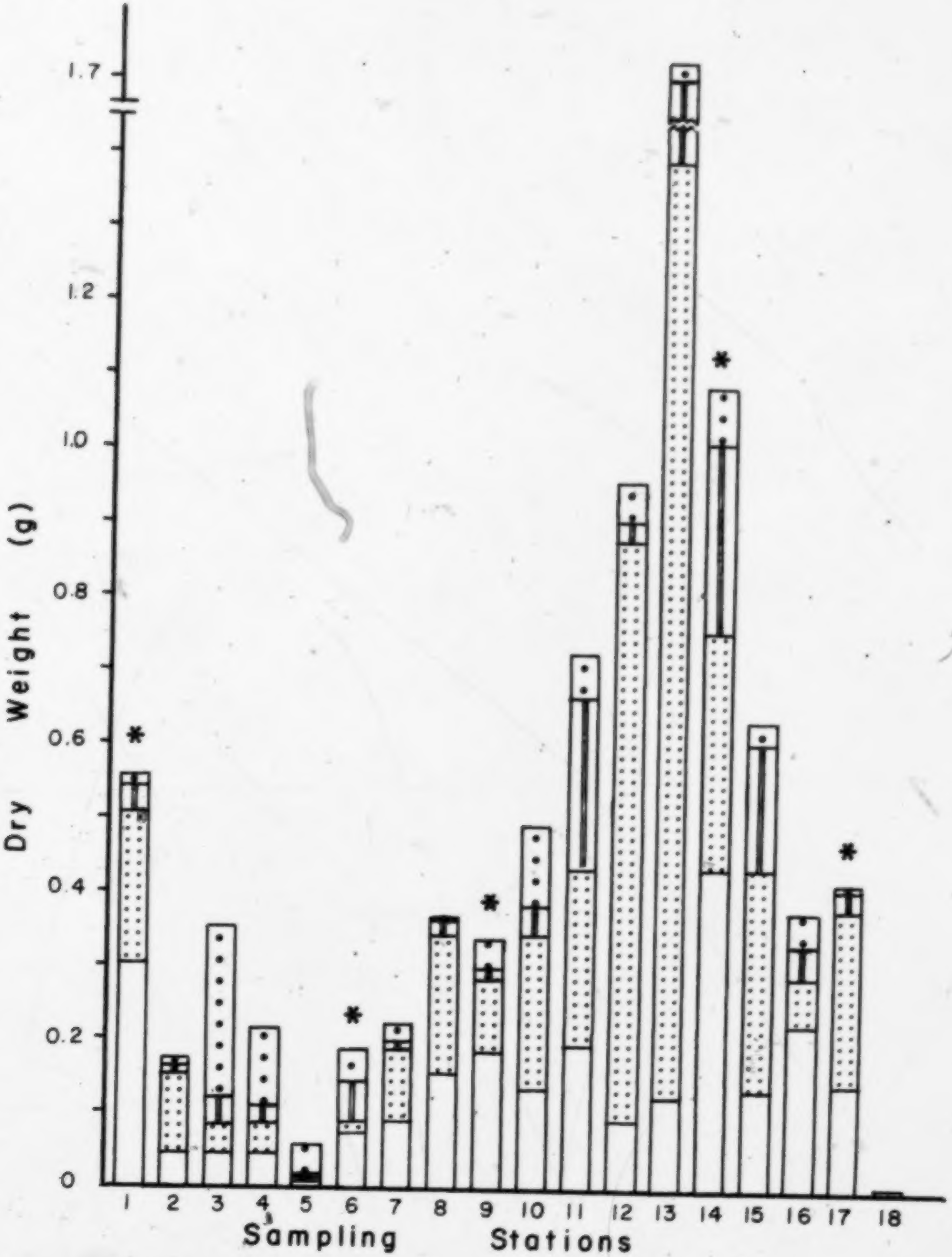

Dry Weight (g)
1.7
1.2
1.0
0.8
0.6
0.4
0.2
0
*
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Sampling Stations

Figure 15. Dry weight of stream bottom samples obtained between 31 May and 2 June, 1976, from the Sheep River, Gorge Creek and Dyson Creek. Forage ratios (Table 21) were based on data recorded at stations 2 and 4 on the Sheep River. Blank portions of figure represent the weight of Ephemeroptera, close stippling represents Plecoptera, vertical lines represent Trichoptera, and the large dots represent other taxa. The numbers of the stations increase as one heads upstream on each stream.

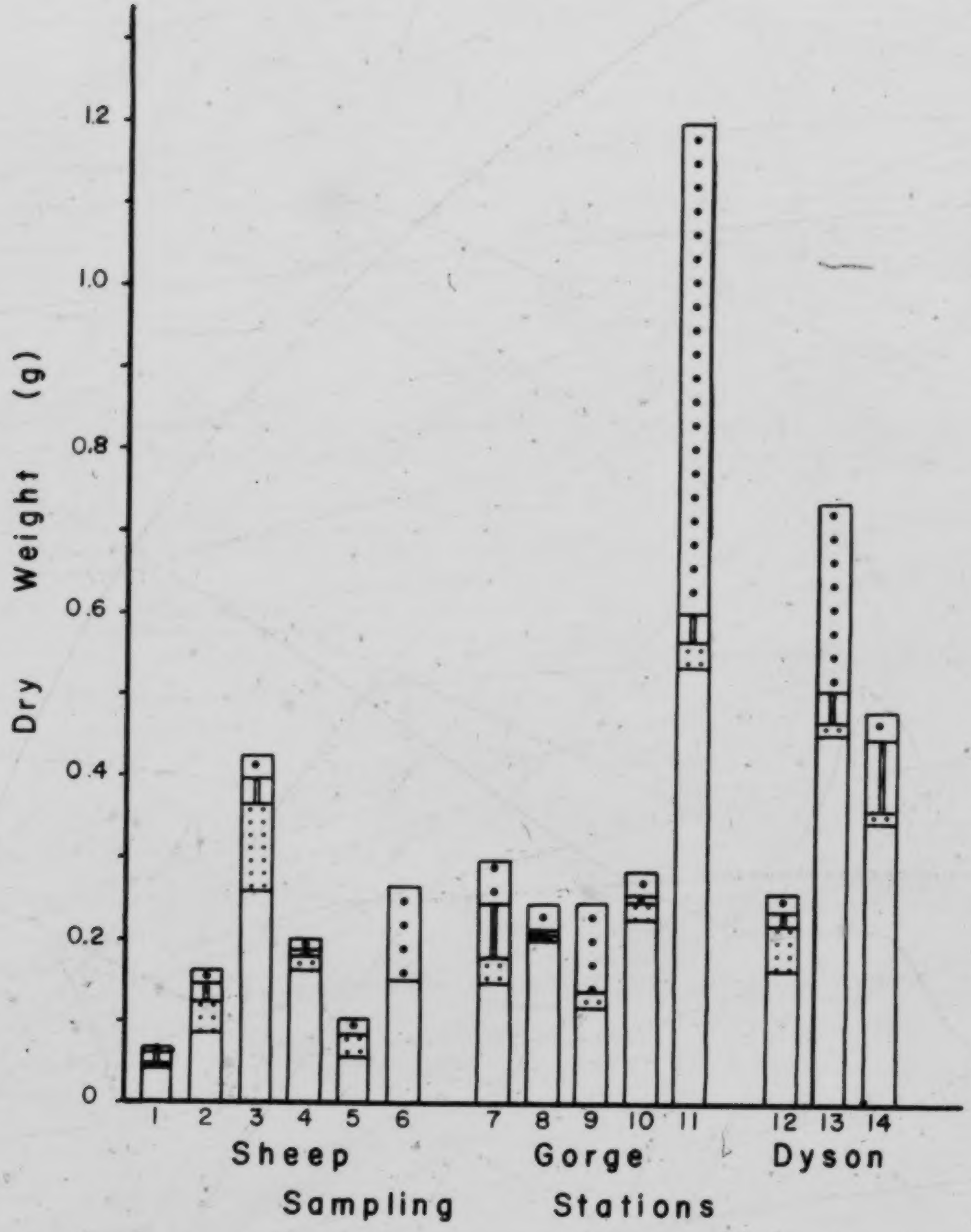

Dry Weight (g)
0
0.2
0.4
0.6
0.8
1.0
1.2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Sheep
Gorge
Dyson
Sampling Stations

Figure 16. Dry weight of stream bottom samples obtained between 1 and 4 July, 1976, from the Sheep River, Gorge Creek and Dyson Creek. Forage ratios (Table 21) were based on data recorded at at station 2 on the Sheep River. Blank portions of figure represent the weight of Ephemeroptera, close stippling represents Plecoptera, vertical lines represent other taxa. The numbers of the stations increase as one heads upstream on each stream.

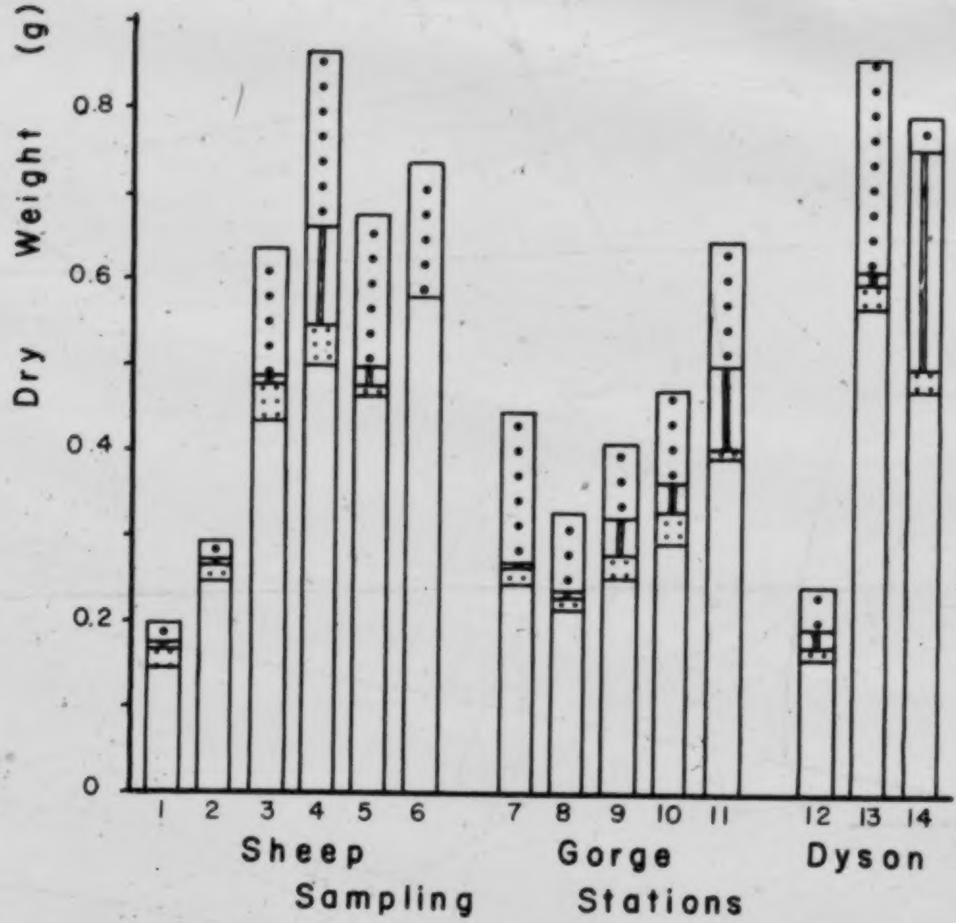

Dry Weight (g)
0.8
0.6
0.4
0.2
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Sheep
Gorge
Dyson
Sampling Stations

Table 17. Comparison of standing crop index of benthic invertebrates among streams and among sampling times using a t-test. Probability values are shown in body of table.

Sampling Stations	Sheep River		Gorge Creek		Dyson Creek	
	June	July	June	July	June	July
Sheep May[1]	$0.1>p>0.05$	>0.1	>0.1	>0.1	>0.1	>0.1
Sheep June		<0.05	>0.1	<0.05	>0.1	$0.1>p>0.05$
Sheep July			>0.1	>0.1	>0.1	>0.1
Gorge June				>0.1	>0.1	>0.1
Gorge July					>0.1	>0.1
Dyson June						>0.1

[1] Only those stations sampled in May on the Sheep River that were similar to or near the stations sampled later in the summer were used in the comparisons (see Fig. 14).

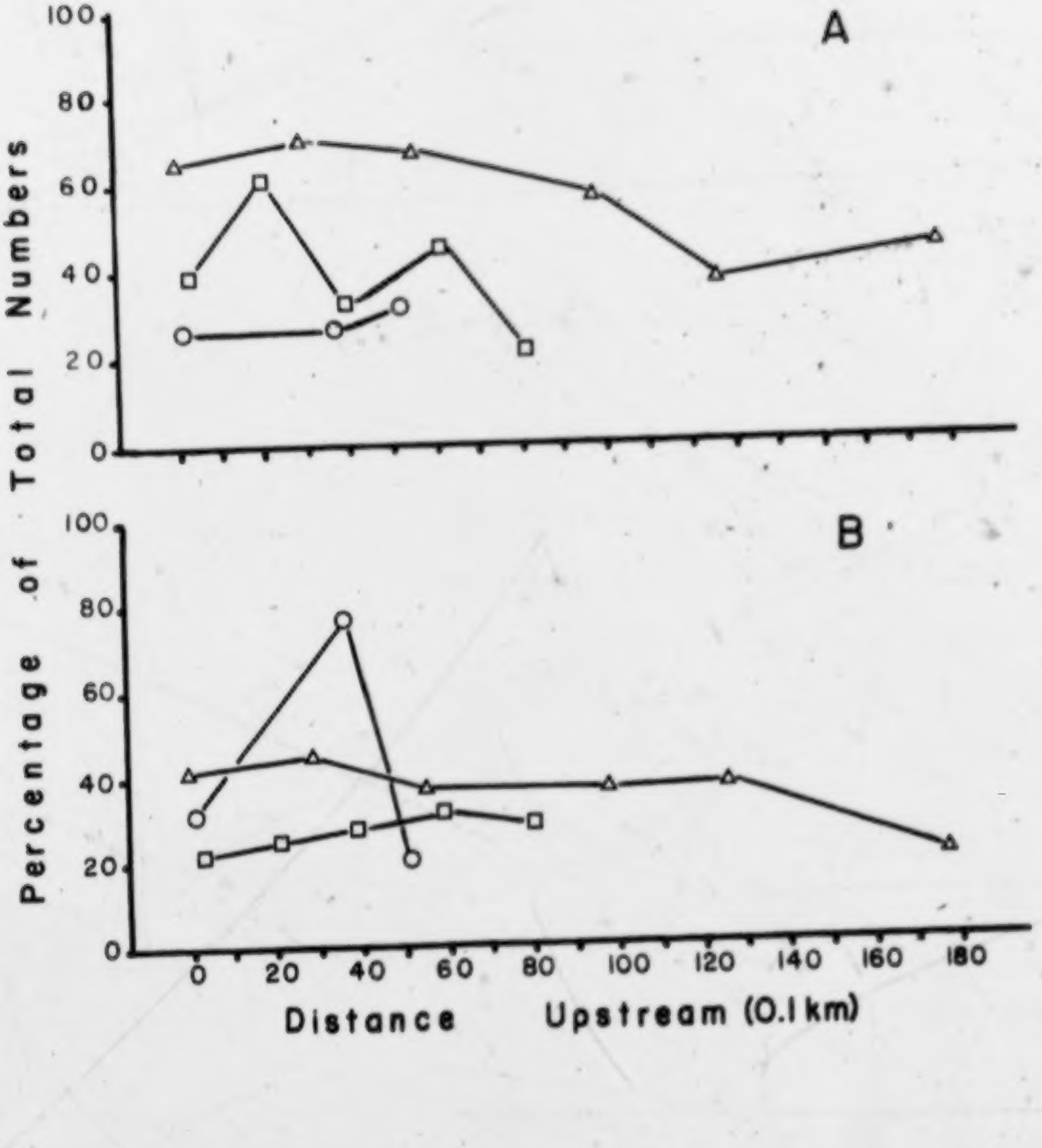
occurred relative to winter biomass levels. Within the breeding season a general trend is discernible; early May and early July are periods of higher standing crops, and no decline into mid-summer was apparent. This difference, in occurrence of a decline, between the Colorado study and the Alberta study may have some bearing upon post-breeding movements of Dippers.

Price (1975) attributes the post-breeding movements of a substantial proportion of residents, to there being a lack of available moulting cover, and a low standing crop of benthic invertebrates in mid-summer on the study area. These movements were upstream, even though there was similarly abundant cover downstream of the study area. Price explains this as a response to higher availability of suitable sized benthic invertebrates upstream and on the basis that invertebrates should be emerging later because of the harsher conditions and later spring break-up.

Because of the harsher conditions at higher altitudes, benthic invertebrates take longer to develop at these altitudes (Hynes 1970). There also is a considerable spread in emergence times for different species from streams in the Alberta study area during the ice-free period (Hartland-Rowe 1964). For example, certain species overwinter as immatures before emerging in very early spring, while others develop from overwintering eggs and emerge in late summer, or early fall. These emergence times would all be expected to shift at higher altitudes so that a spread of emergence times would be maintained. Price (1975) believed larger size categories were more available at higher altitudes in mid-summer. Without more quantitative data, such as samples of benthic invertebrates sorted into size categories, for upstream, downstream, and study area locations, I feel that it was unreasonable for Price to claim that food levels were attracting the Dippers specifically to the upstream reaches. Certainly in the Alberta study area there was no greater decrease in the proportion of smaller insects at upstream locations, compared with stations at lower altitudes, as the summer advanced (Fig. 17). Nonetheless, there was a decline of food in the Colorado study area to which the Dippers may have responded, in addition to the lack of cover, when they moved off their territories. A similar decline in biomass did not occur on the Sheep River study area and there was no comparable movement away from the study area. Therefore, the presence of the required escape cover and a good food supply appear to have enabled Dippers on the Sheep River to stay on the study area during the moulting period, when the demand for good nutrition is particularly high (Newton 1968, Spearman 1971).

Dippers are generally characterized as having an opportunistic foraging strategy, and that selection of prey is related to ease of capture of invertebrates and their abundance in the stream (Goodge 1959, Mitchell 1968, Thut 1970, Sullivan 1973, Price 1975). Reports of stomach contents of Dippers during the breeding season are rare

Figure 17. Percentage of total numbers of invertebrates that were less than 5 mm in length. A - June samples. B - July samples. Triangles indicate stations on the Sheep River, boxes indicate stations on Gorge Creek and circles indicate Dyson Creek. (Essentially only two size classes of invertebrates were found in any numbers in the samples: less than 5 mm and between 5 and 15 mm.)


A
B
Percentage of Total Numbers
100
80
60
40
20
0
Distance Upstream (0.1 km)
0
20
40
60
80
100
120
140
160
180

(Bakus 1959a); most of this type of information comes from winter studies (Mitchell 1968, Thut 1970). I examined stomach contents from six Dippers shot or netted during the breeding season to assess the apparent foraging strategy.

The stomach contents were identified to family or genus (species where possible) (Table 18) by comparison with a reference collection obtained from the benthic samples. All food samples from Dippers were removed within an hour of killing. Some post-mortem digestion occurred (Dillery 1965), but the degree was small and independent of method of handling. I found no soft-bodied invertebrates in any stomach examined even when the stomach contents were preserved immediately. This observation agrees with winter feeding studies (Mitchell 1968, Thut 1970). Thus Dippers probably do not eat soft-bodied taxa in any numbers. Nearly all of the taxa recorded as food for Dippers (Table 19) have some sclerotized body parts which are not easily digested and which can be used for identification, for example head capsules of Chironomidae, mandibles and maxillae of immature, and wings of adult Plecoptera, Trichoptera, and Ephemeroptera. Therefore, few taxa were likely missed as a result of possible post-mortem digestion.

The Dipper stomachs examined contained parts of 12 to 93 prey items (Table 18). The numbers of individual food items in a stomach were comparable with those found in other studies (Table 19), although there were several instances in the latter studies of Dipper stomachs containing over 100

Table 18. Numbers of items in the stomachs of six Dippers collected from the Sheep River, 1976.

Taxa	Birds *1*	*2*	*3*	*4*	*5*	*6*
Ephemeroptera:						
Cinygmula			8	27		
Ameletus	16		42	12	6	2
Ephemerella				4		
Rithrogena			8	1	6	2
Baetis			1	28	4	
Epeorus subg. *Ironopsis*		3	2		5	4
Epeorus subg. *Iron*			2			
Plecoptera:						
Alloperla	1	1	1			
Brachyptera				1		
Arcynopteryx			1		2	2
Nemoura S.	1		1			
Nemoura H.	3					
Adults	2					
Trichoptera:						
Rhyacophila hyalinata	2	4			5	1
R. *verrula*			1			
R. *acropedes*		1		7		
R. unidentifiable						2
Larvae, unknown						5
Adults	6	3		7	17	1
Chironomidae			1			
Formicidae	3			3	1	1
Hymenoptera adult				1		
Diptera adult	3					
Unknown				1		1
TOTAL	37	12	67	93	46	21

Table 19. Animal taxa reported as items found in Dipper stomachs.

Taxa	No. of Stomachs for Which Taxa Recorded Mitchell (1968)	Thut (1970)	Bakus (1959a)	This study
Ephemeroptera	24	3	0	6
Plecoptera	19	4	1	6
Trichoptera	26	6	0	5
Chironomidae	5	3	0	1
Other Diptera	9	3	0	1
Acari	0	5	0	0
Gastropoda	0	5	0	0
Oligochaeta	0	0	1	0
Coleoptera	4	6	1	0
Formicidae	0	0	0	4
Other Hymenoptera	0	0	0	1
Fish	8	0	0	0
No. of Dippers examined	26	6	2	6
Range: No. items/stomach	12-328	45-282	0-3	12-93

items; in each of these cases there were extremely high numbers of a single taxon. Mitchell (1968) found that small prey, usually occurring in clumps in the stream, made up the bulk of the items in 4 stomachs of 26 that contained more than 100 organisms. Thut (1970) found over 100 items in four of the six stomachs he examined and generally one taxon made up the bulk of these 100.

I calculated forage ratios for each of the taxa found in Dipper stomachs using the formula:

$$\text{F.R.} = (t_i / t_a) / (s_i / s_a)$$

where t_i is the number of items of a particular taxon in the stomach, t_a is the number of all items in the stomach, s_i is the number of the specific taxon in the stream samples, and s_a is the number of all items in the stream samples (Hess and Swartz 1941). Forage ratios were determined from all of the stomach contents, rather than for individual Dippers, because the low numbers in the latter instances led to unreasonably high forage ratio values. I sorted all samples obtained at about the same time and nearest to the locations where Dippers were killed (Figs. 14-16, Table 20). The forage ratios covered a wide range (Table 21). A forage ratio of greater than 1 indicates that there is some selection for the taxon considered; whereas a forage ratio of less than 1 indicates that there is avoidance or at least no selection of that taxon (Hess and Swartz 1941). There were only eight items found in Dipper stomachs which were not found in the riffle areas sampled; of these eight, five

Table 20. Number of invertebrates of different taxa found in samples from stations along Sheep River near in time and location where Dippers were killed for analysis of stomach contents.

	Sampling Stations			
Taxa	May 95.5 km	June 97.9 km	June 29.0 km	July 29.0 km
Ephemeroptera				
Cinygmula	582	1629	307	487
Ameletus	4	57	20	2
Ephemerella	66	9	33	32
Rithrogena	102	15	9	8
Baetis	44	147	27	144
Epeorus subg. *Ironopsis*	2	-	1	-
Epeorus subg. *Iron*	12	66	1	30
Stenonema	-	-	1	-
Unknown	-	-	1	-
Plecoptera				
Alloperla	-	30	2	13
Brachyptera	12	-	-	-
Chloroperlinae	4	18	2	-
Arcynopteryx	22	-	4	1
Nemoura S.	134	12	1	-
Nemoura H.	26	-	-	1
Peltoperla	-	3	-	-
Unknown	6	18	4	4
Adults	8	-	-	3
Trichoptera				
Parapsyche A	6	-	-	-
Parapsyche B	2	3	1	-
Rhyacophila hyalinata	14	-	3	1
Rhyacophila sp. 1	4	-	1	-
Rhyacophila verrula	2	6	-	1
Rhyacophila acropedes	-	3	-	-
Rhyacophila alberta	-	3	6	5
Larvae, unknown	2	-	-	-
Pupae, unknown	28	-	-	-
Adults	8	-	-	-
Oligochaeta	-	9	-	1
Diptera				
Pupae	8	-	-	7
Chironomidae larvae	-	18	9	15
Tipulidae larvae	6	9	6	3
Empididae larvae	-	6	-	-
Ephydridae larvae	-	3	-	2
Unknown larvae	-	9	1	-
Adults	40	-	4	30
Coleoptera	2	-	-	1
Corixidae	8	-	-	-
Arachnoidea	-	3	-	1
Formicidae	4	18	2	2
Chilopoda	-	6	-	-
TOTAL	1160	2106	446	776

Table 21. Forage ratios for insects fed upon by Dippers. See text for description of forage ratio.

Taxa Found In Stomachs	Number In Stomachs	Proportion Of Total In Stomachs	Number In Stream Samples	Proportion Of Total In Stream	Forage Ratio
Ephemeroptera	183	0.663	3838	0.904	0.733
Cinygmula	35	0.127	3005	0.708	0.179
Ameletus	78	0.283	83	0.020	14.15
Ephemerella	4	0.015	140	0.033	0.45
Rithrogena	17	0.062	134	0.032	1.94
Baetis	33	0.120	362	0.085	1.41
Epeorus subg. *Ironopsis*	14	0.051	3	0.0007	72.86
Iron	2	0.007	109	0.026	0.0003
Plecoptera	16	0.058	315	0.074	0.784
Alloperla	3	0.011	45	0.011	1.00
Brachyptera	1	0.004	12	0.003	1.33
Arcynopteryx	5	0.018	27	0.006	3.00
Nemoura S.	2	0.007	147	0.035	0.200
Nemoura H.	3	0.011	27	0.006	1.83
Adults	2	0.007	11	0.003	2.33
Trichoptera	62	0.225	99	0.023	9.78
Rhyacophila hyalinata	12	0.043	18	0.004	10.75
R. verrula	1	0.0036	9	0.002	1.80
R. acropedes	8	0.0290	3	0.0007	41.43
R. unidentifiable	2	0.007	-	-	-
Larvae unknown	5	0.018	-	-	-
Adults	34	0.0123	8	0.0018	68.33
Chironomidae	1	0.004	42	0.010	0.400
Formicidae	8	0.029	26	0.006	4.83
Hymenoptera adult	1	0.004	-	-	-
Diptera adult	3	0.011	74	0.017	0.65
Unknown	2	0.007	-	-	-
TOTAL	276	1.0	4285	0.952	
Taxa not taken			215	0.048	

were case-dwelling caddisfly larvae typically found in pools (Pennak 1953). This indicates that Dippers forage mostly at fast-moving riffles and that the stream samples provided good quantitative estimates of food available where Dippers generally foraged.

The forage ratios for the Plecoptera and Ephemeroptera indicated less selection than one would expect from their abundance in the stream, while the Trichoptera were highly selected. Mitchell (1968) found a similar preference for Trichoptera over Plecoptera and Ephemeroptera during the winter. Despite these generalizations, certain taxa within these orders had forage ratios different from those of the order as a whole, again similar to the observations of Mitchell (1968).

Among the Ephemeroptera, four taxa were taken in excess of their general availability in the stream: Epeorus subg. Ironopsis, Ameletus, Rithrogena, and Baetis (in decreasing order of selection). Similarly for Plecoptera, three taxa were preferentially selected: Arcynopteryx, Nemoura H., Brachyptera. The low representation of Trichoptera in stream samples may have produced misleadingly high forage ratios, but there is probably some real selection, particularly for Rhyacophila hyalinata.

The apparent selection for Plecoptera and Trichoptera adults and the Formicidae (ants) was likely an artefact of the stream sampling method. These taxa could not be sampled, quantitatively, from the areas where Dippers were observed catching them i.e. on exposed rocks, the stream banks, and cliff faces. They were more abundant in these regions than as debris or drift obtained during sampling. In the ice-free season, Dippers were able to take advantage of these aerial and terrestrial food resources. Sullivan (1973) documented a changing pattern of foraging maneuvers during the four seasons which was related to the appearance of these resources. He observed that, in the spring and summer, much more terrestrial foraging occurred than in the fall and winter.

The most important selection is that involved with the bulk of the food items, that is, the immature insects. The selection observed appeared to be related to two major factors: conspicuousness of the insect and probable ease of capture. Except for Ameletus and Baetis, all of the Ephemeroptera and Plecoptera were dorso-ventrally flattened. Ameletus and Baetis are free-ranging genera of rapid water which maintain themselves in the current by clinging to rocky substrate, yet by means of darting movements they can move about in spite of the current. The remaining Ephemeroptera and Plecoptera are slower moving, cling to the rocks to avoid being swept away, and are frequently found on the undersides of rocks or in crevices (Pennak 1953). Except for the Nemoura spp. which are detritivores or herbivores, the Plecoptera are carnivorous and therefore more mobile and probably more conspicuous than the generally herbivorous Ephemeroptera.

All invertebrates sampled were roughly measured and placed into four size categories: (1) <5 mm, (2) 5 to 15 mm, (3) 15 to 25 mm, and (4) >25 mm. Cinygmula specimens were the smallest and generally accounted for all Ephemeroptera in the smallest size class, although some were put into the second class. Ephemerella and Epeorus subg. Iron were also quite small, with some less than 5 mm and most slightly larger than 5 mm. Epeorus subg. Ironopsis and Rithrogena were quite large, generally being placed in the upper half of the second size class. Baetis and Ameletus were always larger than 5 mm but in most cases smaller than 10 mm. Similarly among the Plecoptera, the largest taxa were the ones selected i.e. Arcynopteryx, Nemoura H., and Brachyptera. Nemoura H. was not much larger than Nemoura S. nor Alloperla, but unlike these two which had smooth exoskeletons, Nemoura H. was covered with densely packed, very conspicuous dark setae. Therefore, the taxa of Ephemeroptera and Plecoptera that were selected were larger or more conspicuous by their actions or exterior (Ameletus, Baetis, Nemoura H.) than those that were not selected.

Rhyacophila spp. represented the major taxon of Trichoptera consumed. The five unidentified Trichoptera larvae were case-dwelling and likely pool-dwelling, while the rhyacophilids were free-living forms found in the riffles. The Dippers did not appear to be selecting pool-dwelling taxa in favour of riffle-dwelling taxa as Thut (1970) found for Dippers during the winter, in Washington.

This may be a result of differences in stream morphometry between the two study areas, however, it may also partly be a result of the differing sampling procedures used.

Despite the discrepancy between stream sampling times and locations relative to the times and locations that birds were killed in Mitchell's (1968) study, her results on the winter food of Dippers are in general agreement with mine. Dippers appeared to select the larger, more conspicuous food items in the Montana study area. Some Dipper stomachs examined by her contained numerous very small prey items which were often found in clumps in the stream.

I did not find fish in the Dipper stomachs, although I had observed Dippers, eating fish, apparently fingerling trout, twice during this study. Thut (1970) found no fish in stomachs he examined, even though the Dippers were caught because some had been eating fingerling trout in an experimental study stream. Thut concluded that fingerling trout were normally not available. Mitchell (1968) found that only those Dippers caught on the stream from which she had sampled fish had fish in their stomachs.

Records of Cinclidae eating fish are numerous (Michael 1922, Cordier 1927, Bent 1948, Bakus 1959a, Pastukhov 1961, Sullivan 1973, Jost 1975), In fact, Jost (1975) describes fish otoliths in pellets regurgitated by _C. c. cinclus_; throughout my study I saw no pellets nor any behaviour resembling casting of pellets. It is unlikely this behaviour is peculiar to _C. cinclus_ and may more likely be a result of a high proportion of fish in the diet which would require the elimination of scales. Dippers probably eat fish only when fish are abundant or in a situation that give the birds an advantage (particularly in hatcheries, Munro 1924, 1936).

Dippers have a variety of foraging methods which enable them to exploit the stream fauna. Sullivan (1973) describes several types: aquatic foraging (wade-dive, head-dip, swim-dive, swim-pick, plunge-pick), terrestrial foraging (surface picking, detritus or rock turning) and aerial foraging (flycatching by hawking from a perch). During over 90 days of observations I saw Dippers forage in all of these manners, although swim-picking and plunge-picking were rare and aerial flycatching was observed only twice.

A previously undescribed foraging maneuver, hover-picking, was observed in three territories where vertical, sheer cliff faces were abundant. When hover-picking, Dippers would perch on a small ledge, or occasionally on a nearly vertical face like a swallow, scan the rock above, fly up and hover momentarily while picking off an insect, and then drop to the same or another perch. This type of foraging appeared to be quite successful; often a Dipper might hover-pick for several minutes before changing to another foraging pattern.

Because of the distance from which I usually observed the birds, I could not determine, in many cases, whether a particular foraging maneuver had been successful.

Therefore, I focused on data of the frequency of occurrence in order to assess importance of particular foraging patterns.

In the course of foraging, a Dipper might specialize for a period, but also would frequently vary its maneuvers. Overall, there was considerable variation in foraging maneuvers used (Tables 22, 23).

Certain foraging maneuvers were observed to be dependent on time of day (Table 22). Both hover-picking and terrestrial foraging were used by the Dippers less frequently than expected during the early morning hours. When Dippers used these foraging maneuvers they were generally catching winged adults that were resting on rocks and cliff-faces; these insects did not start flying until the air temperature was sufficiently high. This would also explain the less than expected use of hover-picking during the early to late evening periods, for the temperature decreases during these periods. Terrestrial foraging occurred more than expected in the late evening, which probably reflected the greater conspicuousness of winged adults on the whitish, shore-line rocks, than insects in the water. Wade foraging was used more frequently than expected between 09:00 and 12:00, but less frequently than expected between 12:00 and 15:00. The reverse was true of drift-line foraging. These foraging maneuvers, although different in procedure, often occurred in neighbouring locations. The increased use of these foraging movements, in mid-morning,

Table 22. Number of 20-second intervals each foraging maneuver observed[1] during five periods over the day. Expected values and results of X^2 test are also shown.

Foraging Maneuver		0500 to 0900	0900 to 1200	1200 to 1500	1500 to 1800	1800 to Dusk	X^2
		Time of Day					
Wade	O[3]	74.0	117.0	37.0	76.0	27.0	171.4
	E	75.8	85.5	59.8	76.0	33.9	d.f.=24
							0.01>p
Swim-dive	O	74.0	77.0	33.0	76.0	21.0	
	E	64.4	72.6	50.8	64.6	28.8	
Swim-pick	O	9.0	8.0	9.0	7.0	1.0	
	E	7.8	8.8	6.1	7.8	3.5	
Plunge-dive	O	44.0	51.0	29.0	34.0	15.0	
	E	39.6	44.7	31.3	39.7	17.7	
Terrestrial	O	40.0	68.0	61.0	45.0	41.0	
	E	58.4	65.8	46.1	58.6	26.1	
Hover-pick	O	1.0	20.0	3.0	30.0	1.0	
	E	12.6	14.2	9.9	12.6	5.6	
Drift-line	O	80.0	22.0	82.0	55.0	38.0	
	E	63.4	71.5	50.0	63.6	28.4	

[1] Observations were lumped for four birds from two territories observed in 1975.

[3] O-Observed values; E-Expected values from the X^2 contingency table.

Table 23. Number of 20-sec intervals each foraging maneuver was observed[1] in each month. Expected values and X^2 test results are also shown.

Foraging Maneuver		Month May	June	July	August	X^2
Wade	O[3]	32.0	161.0	81.0	28.0	453.7
	E	42.3	81.7	132.2	45.9	d.f.=18 0.01>p
Swim-dive	O	55.0	69.0	105.0	56.0	
	E	39.9	77.1	124.8	43.3	
Swim-pick	O	6.0	27.0	14.0	0.0	
	E	6.6	12.7	20.6	7.1	
Plunge-dive	O	13.0	14.0	114.0	44.0	
	E	25.9	50.0	81.0	28.1	
Terrestrial	O	53.0	83.0	80.0	11.0	
	E	31.8	61.4	99.4	34.5	
Hover-pick	O	29.0	0.0	25.0	1.0	
	E	7.7	14.9	24.1	8.4	
Drift-line	O	2.0	13.0	175.0	66.0	
	E	35.8	69.2	112.1	38.9	

[1] Observations were lumped for four birds from two territories observed in 1975.

[3] O-Observed values; E-Expected values from X^2 contingency table.

possibly reflected the increased light relative to earlier in the day. A reduction of use of wade and swim-dive foraging maneuvers during the subsequent time period likely reflected the efficiency of the earlier bouts. A concurrent, relative increase in drift-line foraging during the latter period may have been in compensation for reduced efficiency when using swim-dive or wade foraging.

The prevalence of particular foraging maneuvers differed between the two pairs observed ($X^2=101$; $p<0.005$). I observed the pair at Underground Streams foraging along the drift-line (edge of stream) only once, while the pair at Bridge Falls frequently foraged along the drift-line. In addition, the pair at Underground Streams used the terrestrial foraging maneuver relatively more frequently.

Considerable variation in composition of foraging maneuvers occurred over the summer (Table 23). Drift line foraging was most responsible for this difference, as it occurred much less frequently than expected during May and June, but much more frequently than expected during July and August. This change in prevalence of drift-line foraging was likely in response to an increased abundance of dead flying insects being caught by the backwaters and eddies and swept towards the shore-line.

There was a general increase in foraging in July (and August for Bridge Falls) which reflected the period of hatching and nestling development (Table 24). This increase in frequency of foraging occurred throughout the territory;

Table 24. Percentage time spent foraging throughout the day during each month, for two pairs of Dippers observed in 1975.

Location	Dipper	Month	Percentage of Time Spent Foraging
Underground Streams	unbanded male	June	11.7
	0915 female	June	2.1 (13.9)[1]
		July	12.1 (22.3)
Bridge Falls	0920 male	May	8.2
		June	3.5
		July	35.3
		August	54.6
	0901 female	May	13.8 (19.5)
		June	2.3 (7.8)
		July	3.2 (20.3)
		August	28.3 (96.3)

[1] Numbers in brackets are percentages of time spent foraging by females relative to a total time observed outside the nest, as opposed to the other value which is based on a total time during which the bird was observed plus the time when it was known to be in the nest.

often the Dippers would fly a few hundred meters from the nest to forage.

There were some individual differences in frequency of certain foraging maneuvers. The members of the pair at Underground Streams differed in the frequency with which they used certain foraging maneuvers ($X^2=14.3$; $0.025>p>0.01$), but not to the same extent as between the male and female at Bridge Falls ($X^2=251$; $p<0.005$). At Bridge Falls, the female (0901) used three foraging maneuvers most frequently: wade, terrestrial, and drift-line foraging (in decreasing order of frequency). The male (0920) similarly used drift-line, swim-dive, and plunge-dive foraging (in decreasing order of frequency). Although the data are few, they suggest that some separation of the food available within a territory may be occurring through use of different foraging techniques. Such intersexual differences in foraging have been observed for a woodland nesting passerine, the Red-eyed Vireo (*Vireo olivaceus*) (Williamson 1971). It may be that the inter-sexual differences noted for the Dippers are simply individual preferences. Further data are warranted before strong conclusions can be made concerning this aspect of Dipper foraging.

Overall, the Dippers appear to make use of a variety of foraging maneuvers and to make use of each repeatedly; these are: wade, swim-dive, drift-line, terrestrial, plunge-dive, hover-pick, swim-pick, and fly-catch (in decreasing order of frequency). The difference in foraging patterns between different birds may be a result of different habitat structure which affects proportions of foraging areas suitable for certain types of foraging (this would explain inter-territory differences), or a result of separation of use of the resource, which may improve overall foraging efficiency (as between members of a breeding pair).

It remains then to try to resolve which type of foraging strategy may be exhibited by Dippers. Both Mitchell (1968) and Thut (1970) suggested that the birds' seemingly opportunistic behaviour is in accord with Tinbergen's hypothesis (Gibb 1962) of a search image. The Dippers may form an image of a particular prey which they then search for during a particular foraging bout. A different model of foraging strategy suggests that birds forage optimally (Royama 1970, Hartwick 1976). Although I do not have adequate data on the efficiencies of various foraging patterns, nor on the dietary value of certain sizes or types of prey, the Dipper is clearly a species which may fit a profitability strategy model. Because it has a number of different foraging maneuvers and during its foraging bouts may sample one or several different regions in and around the stream, it has the capacity to sample regions of differing prey density, abundance and composition. It would be reasonable to expect that, during given stream conditions, there may be higher profitability accruing from repeated foraging utilizing one maneuver, while at other times a more frequent change of foraging maneuver may be more efficient. Because of the dynamic nature of the stream environment, it is likely that the Dippers should have evolved a dynamic foraging strategy to meet these changes.

Territory Distribution and Function

Breeding territories were generally established by the Dippers immediately they returned to the study area. At this time there was a large influx of Dippers (Table 4), many of which attempted to establish territories, sometimes for as long as 6 weeks without succeeding (e.g. 4406). Both Sullivan (1973) and Price (1975) report such attempts; the former refers to these attempts as "surplus" nesting attempts. Price (1975) estimates that between 13 and 29% of all birds that were seen attempting to breed on his study area were surplus, in that they attempted to breed (they were observed singing, starting nest building, courting, or attempting to establish territories), failed, and moved off the study area.

Before considering the presence and nature of a surplus of Dippers in the Sheep River population, an examination of parameters which may govern the establishment of territories (as suggested by Lack 1966) is presented. I was unable to determine consistent territory boundaries for several of the breeding pairs in 1975. Therefore, consideration of most features of the territories was based upon the 1976 data. The distribution of territories (Figs. 18-20) was similar to that described for other cinclid populations (Robson 1956, Bakus 1959b, Balat 1962, 1964, Hewson 1967, Shooter 1970, Sullivan 1973, Klein 1974, Price 1975, Sunquist 1976), that is, the birds were widely distributed during the breeding

Figure 18. Map showing extent of 1976 breeding territories of Dippers on the Sheep River. Approximate locations of nest sites are opposite names of sites. Cross-hatched area includes stream length contained within each territory. Solid lines indicate territory boundaries, dotted line indicates unconfirmed boundary. Asterisks indicate nests used in 1975, but not in 1976.

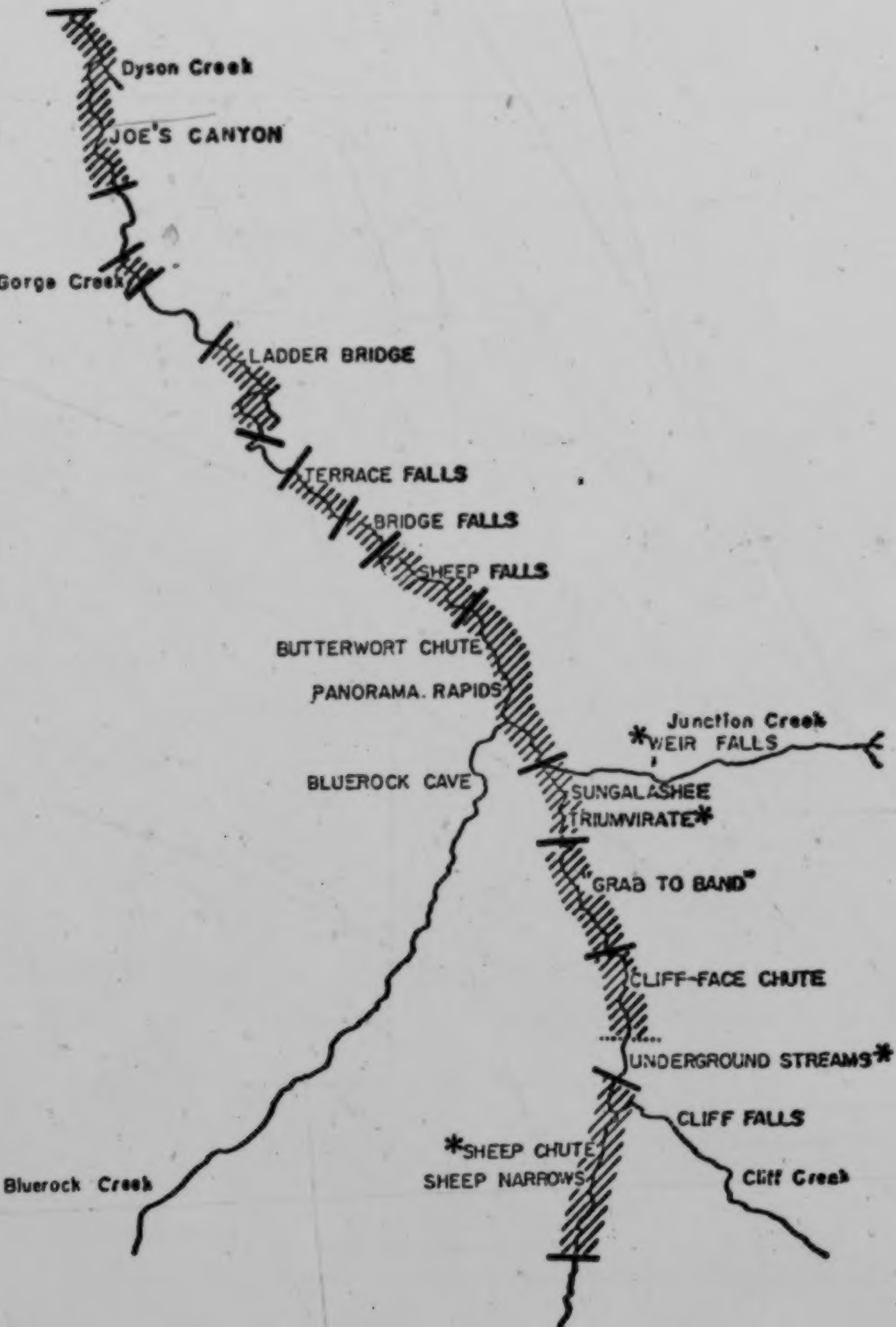

Dyson Creek
JOE'S CANYON
Gorge Creek
LADDER BRIDGE
TERRACE FALLS
BRIDGE FALLS
SHEEP FALLS
BUTTERWORT CHUTE
PANORAMA RAPIDS
Junction Creek
*WEIR FALLS
BLUEROCK CAVE
SUNGALASHEE
TRIUMVIRATE*
"GRAB TO BAND"
CLIFF-FACE CHUTE
UNDERGROUND STREAMS*
CLIFF FALLS
*SHEEP CHUTE
SHEEP NARROWS
Bluerock Creek
Cliff Creek

Figure 19. Map showing extent of 1976 breeding territories of Dippers on Gorge Creek. Approximate locations of nest sites are opposite names of sites. Cross-hatched area includes stream length contained within each territory. Solid lines indicate territory boundaries, dotted line indicates unconfirmed boundary. Asterisks indicate nests used in 1975, but not in 1976.

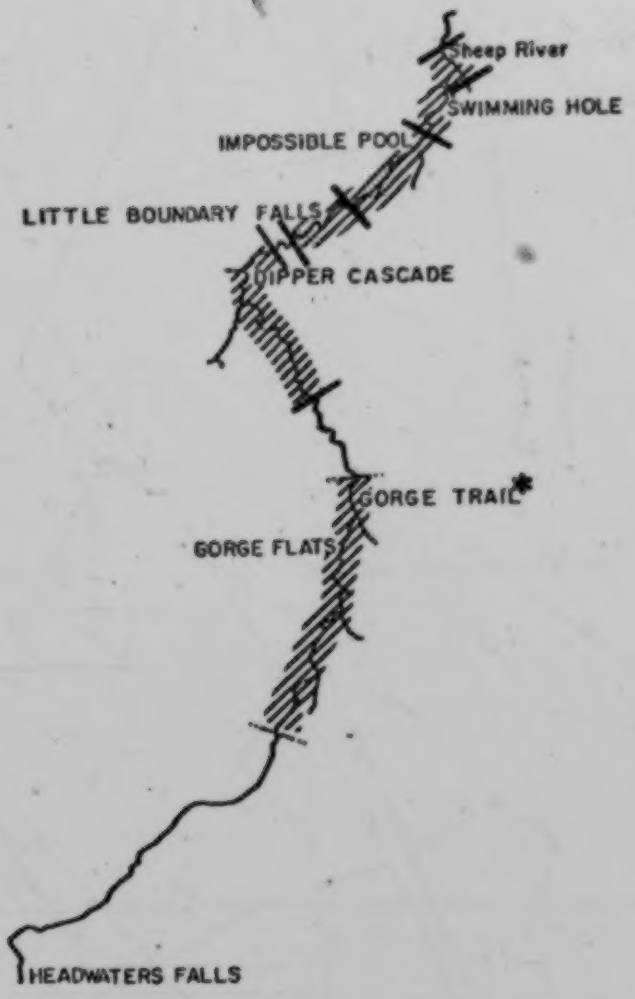
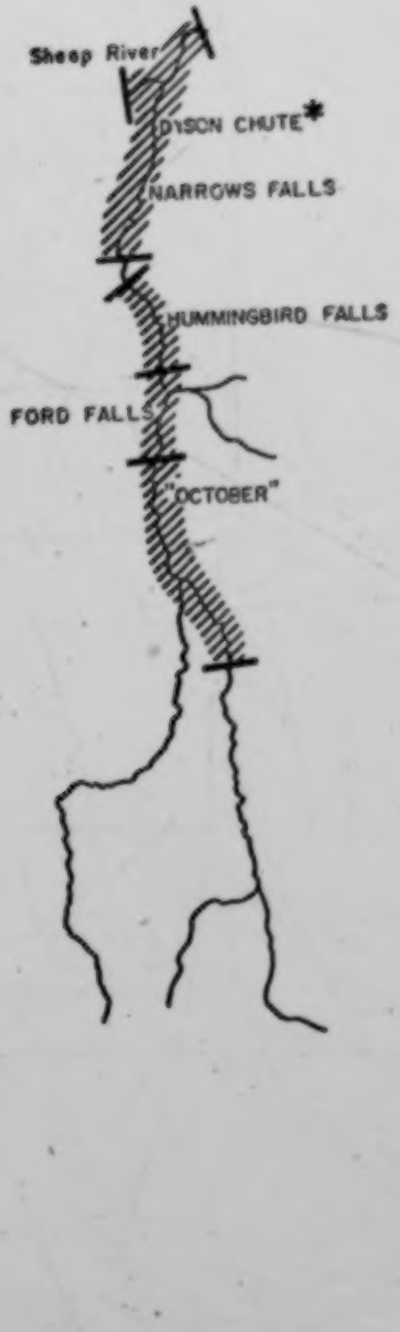

Sheep River
SWIMMING HOLE
IMPOSSIBLE POOL
LITTLE BOUNDARY FALLS
DIPPER CASCADE
GORGE TRAIL*
GORGE FLATS
HEADWATERS FALLS

Figure 20. Map showing extent of 1976 breeding territories of Dippers on Dyson Creek. Approximate locations of nest sites are opposite names of sites. Cross-hatched area includes stream length contained within each territory. Solid lines indicate territory boundaries. Asterisks indicate nests used in 1975, but not in 1976.


Sheep River
DYSON CHUTE*
NARROWS FALLS
HUMMINGBIRD FALLS
FORD FALLS
"OCTOBER"

season, having large, very elongate territories relative to most other passerines (Schoener 1968). There is considerable variation in the lengths of cinclid territories reported (Table 25). One of the perpetual questions in population studies of cinclids has been: what determines the size of breeding territories and hence the number of birds breeding in a particular area?

I examined a number of habitat parameters in describing the study area (see Stream Environment). There was considerable heterogeneity in occurrence of cover, depth and nature of current, and nest site potential (Figs. 6-9). In addition to those parameters, the different streams varied in width as well as in total benthic biomass (Figs. 14-16). I could find no relationship between territory length and benthic biomass (Fig. 21). This agrees with Price's (1975) results. Width of the streams on which the Dippers nested also did not seem to play a role in determining territory size, although the three longest territories were on the narrower tributaries (Table 26). Price (1975) examined a larger sample size of territories than were available in the present study, and found that none of a series of environmental parameters or biological characteristics of the birds were correlated with territory size, except the absence of an adjacent territory at one end. In my study area, of the five territories with lengths over 2 km, four were at the upstream or downstream end of a series of territories. Thus, they were without an adjacent territory

Table 25. Lengths of territories reported in the literature for *Cinclus* spp.

Species and Location	Mean Length of Territory (m)	Range of Lengths (m)
C. mexicanus		
Sheep River (this study)	1406	670-2080
Gorge Creek (this study)	1473	990-2250
Dyson Creek (this study)	2070	910-3910
Boulder, Colorado, U.S.A.		
(Price 1975) monogamous males	944	
polygynous males	2031	
polygynous males[1]	1504	
Missoula, Montana, U.S.A.		
(Sullivan 1973)	759	
(Bakus 1957)	-	max. 350[2]
C. cinclus		
Spessart, West Germany (Klein 1974)	2800	
Czechoslovakia (Balat 1964)	653	350-1250
North Westmorland, U.K. (Robson 1956)	430	110-640
Saxony (Richter 1953)	500-600	
Birks, U.S.S.R. (Dementiev and Gladkov 1954)	2000-3000[3]	
C. pallasii		
Pakistan (Sunquist 1976)	425	315-562

[1] Excludes an unusually long territory which was probably not entirely defended (Price 1975).

[2] Likely an underestimate of territory length resulting from field technique.

[3] Inter-nest distances only.

Figure 21. Mean food biomass of benthic samples obtained within territories, at the times of territory establishment, compared with territory length.

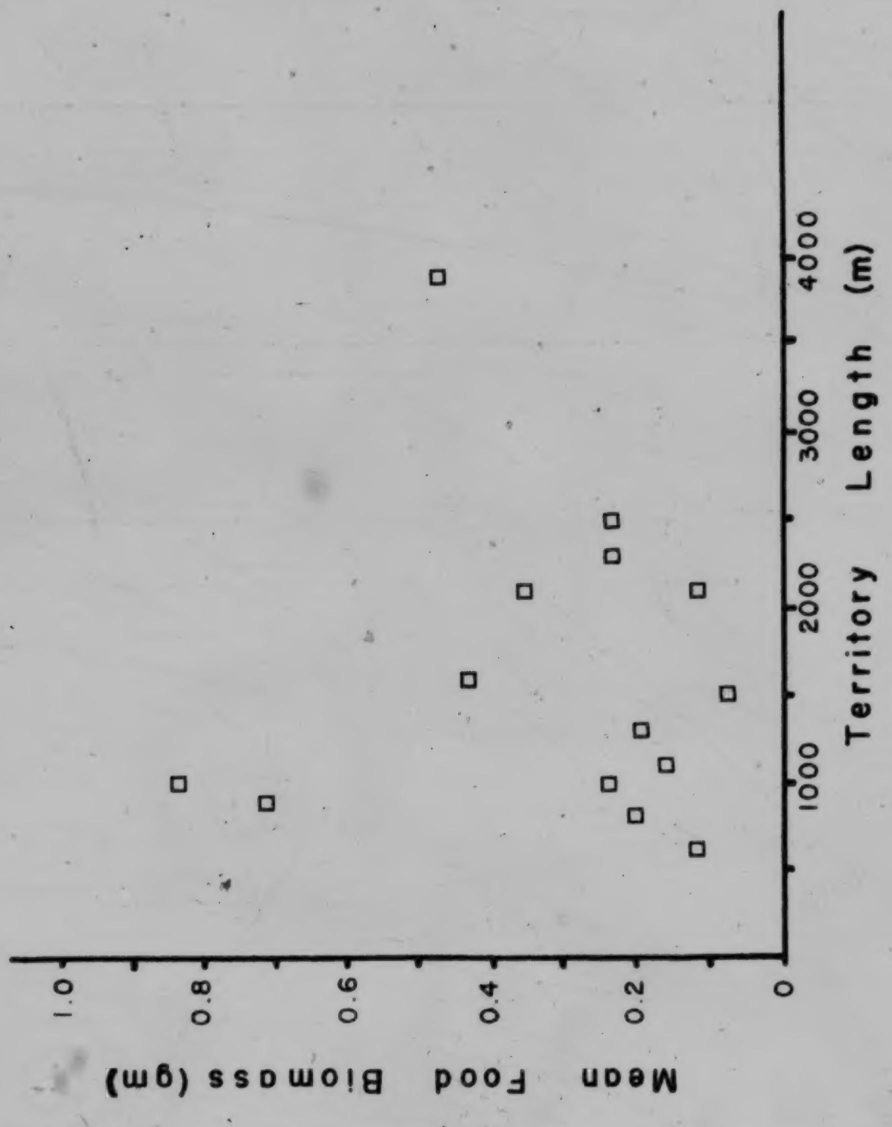

Mean Food Biomass (gm)
1.0
0.8
0.6
0.4
0.2
0
1000
2000
3000
4000
Territory Length (m)

Table 26. Territory sizes calculated for 1976 breeding territories on the Sheep River, Gorge and Dyson Creeks (Figs. 18-20).

Territory	Length (m)
Joe's Canyon	1930
Ladder Bridge	1470
Terrace Falls	670
Bridge Falls	760
Sheep Falls	1060
Butterwort Chute - Panorama Rapids	2050
Sungalashee	1020
"Grab-to-Band"	1620
Cliff-face Chute	undetermined
Sheep Narrows	2080
Sheep River mean	1406
Swimming Hole	1320
Log-jam Narrows (Impossible Pool)	1250
Little Boundary Falls	990
Dipper Cascade	2250
Moss Overhang - G-12 (Gorge Flats)	undetermined
Gorge Creek mean	1473
Narrows Falls	2450
Hummingbird Falls	1010
Dyson Ford Falls	910
"October"	3910
Dyson Creek mean	2070

at one end (Table 26, Figs. 18-20).

Shooter (1970) stated that the availability of food, not total biomass or stream width, determined territory size of the European Dipper. The availability of food depended upon the total amount of preferred foraging areas, that is, shallow stretches of stream (Shooter 1970). He also suggested that about an acre of shallow stream was required by a breeding pair. Klein (1974) provided some qualitative evidence that supports this idea; he found that the longer territories were in areas of deeper, faster-moving water, but he also found that territories were shorter in areas that had a high number of secure nest sites. I found that the total amount of shallow stream within territories was quite variable (Table 27). If there was a minimum amount of shallow foraging areas required by Dippers then there must have been sufficient obtainable food along the shallow edges of the stream, or their requirements for food are smaller than are indicated by the above authors for the European Dipper, or most likely there was sufficient food in deeper sections of stream, which they were capable of obtaining. Observations of a number of territories over a wider range of stream types and food abundance than I had, may support the general arguments of Shooter (1970) and Klein (1974).

Because availability of nest sites has been shown to limit the numbers of several bird species breeding in certain areas (Lack 1954), I felt it important to examine the possibility of excess nests. There were a number of

Table 27. Morphometry indices compared among territories of different sizes on the Sheep River study area.

Stream	Length of Territory	Morphometry Index[1]	Corrected Index[2]
Sheep	1470	8.0	8.0
	670	1.0	1.0
	760	2.4	2.4
	1060	6.6	6.6
	2050	6.5	6.5
	1020	5.2	5.2
	1620	10.8	10.8
Gorge	950	9.5	3.2
	790	7.9	2.6
	1750	17.5	5.8
Dyson	1010	5.1	1.7
	910	9.1	3.0
	3910	37.1	12.4

[1] Morphometric Index is the total number of 100 m sections of stream within a territory that have stream morphometry classifications of 0, 1, or 2; these are the shallowest sections classified (see Fig. 8 for explanation of classification system).

[2] Corrected Index is determined in the same way as Morphometric Index with the exception that all sections on the narrower tributaries are divided by 3 to account for the difference in area between a stretch of stream on the Sheep River and the same length of stream on the tributaries.

unused nest sites within breeding territories in both 1975 and 1976 on the Sheep River study area (Table 28). Not all nest sites were included in this Table because it is unreasonable to expect Dippers to nest within 100 m of each other, given their aggressive nature (the shortest inter-nest distance during my study was 400 m). Other studies also showed that rarely do cinclids nest within 100 m of each other (Robson 1956, Balat 1964, Hewson 1967, Shooter 1970, Sullivan 1973, Klein 1974, Price 1975, Sunquist 1976). One observation of Dippers nesting very close to each other was of two pairs within 50 m of each other at opposite ends of a waterfall (Emily Dixon pers. comm.). Such a large physical feature presumably reduced the interactions between adjacent pairs.

Frequently, I found cliff-faces on which two or more nest sites were located; in each of these instances I counted only one potential site, for reasons presented above. Unused sites have been shown to differ in character, and apparently in quality, from those that were used (see p. 86). Perhaps those sites that were not used were too unsuitable. This might have been true of the six sites that remained unused both years, but would not account for those nests used in 1 of the 2 years. Also, it should be noted that all of these unused sites were obviously used by Dippers in the past, at least to the point of completion of a nest; therefore, there must be some attraction in such sites, which appear then to be excess nests.

Table 28. The number of unused nest sites that were greater than 100 m away from used nests, yet still within the territories of Dippers on Sheep River and Gorge and Dyson Creeks.

Stream	1975 Unused	1975 Used	1976 Unused	1976 Used	1975+1976[1] Unused
Sheep River	5	11	7	10	4
Gorge Creek	2	5	2	5	1
Dyson Creek	2	4	2	4	1
TOTAL	9	20	11	19	6

[1] Nests that were unused during both years.

If one accepts the evidence that there were excess nest sites, sufficiently far apart that aggression involved in maintenance of interindividual distance (King 1973) would not be a problem, then one must ask: why were there not more Dippers nesting there? Were there additional Dippers that had been excluded? Was there a possibility that some Dippers did not breed, if they were excluded?

In an attempt to answer these questions, I removed all Dippers initiating nesting on the Sheep River between the Bridge Falls and Ladder Bridge territory and also between the Butterwort Chute - Panorama Rapids and Cliff-face Chute territories (Fig. 3). I stopped removing Dippers when a third pair had been observed initiating a nest at Terrace Falls (Table 29).

In view of nest failures that may have been related to inexperience (Table 16), I wanted to determine whether the replacement birds were capable of actually breeding. The last replacement pair at Terrace Falls (subsequently banded 4480 and 4481) were successful in raising a brood to fledging. Some of the Dippers establishing the first territories could not be retrieved after they were shot. All but one of the female Dippers that were retrieved had well developed gonads. The single exception (June 15, Terrace Falls - unbanded) had several follicles larger than 2 mm in diameter and a slightly enlarged oviduct. There was no evidence that this bird, nor any of the other replacements might already have bred elsewhere and failed.

Table 29. Results of removal experiment on two portions of the Sheep River, 1976 (see Fig. 3).

Territory	Removal Date	Birds Removed	
		Female	Male
"Grab-to-band"	9 May	0932	4401[1]
	24, 25 May	unband[1]	unband
Sungalashee	10-12 May	4412[1]	0998[1]
	8 June	unband	0916
Terrace Falls	15, 16 May	0902	4414[1]
	15 June	unband	unband
	19 July[2]	4481	4480

[1] Bodies not retrieved after shot.
[2] Date of banding; not removed, permitted to nest.

As indicated earlier (see p. 52) there appeared to be a number of individuals that were actively searching for places to breed and which were being excluded from the study area. It is my argument that this exclusion was a result of the presence of territorial birds. Further evidence suggesting that Dippers may be excluded from breeding, probably by territorial birds, was provided by two banded male Dippers which were not observed as breeding residents in 1975, but which attempted to obtain territories and nest sites on the study area in 1976. Because male Dippers have such a high nest site fidelity (Sullivan 1973, this study), these observations of 0913 trying to obtain a territory on lower Gorge Creek for over 3 weeks and of 0916 replacing birds removed from a territory, strongly suggest that some Dippers may not breed during some years.

Observations of Dippers during the winter was only a casual portion of my research, however, it is significant that during late February the only banded Dipper observed (0998) was found within the boundaries of its subsequent breeding territory, with an unbanded Dipper presumably the unbanded female mate observed with 0998 in early April. During the winter census the upstream territory boundary was roughly the same as subsequently determined during the breeding season (Sungalashee Fig. 18), although a downstream territory boundary could not be determined in February. At this time there were five other Dippers observed where the Sheep River was open; two were downstream near Bluerock

Creek (Fig. 18), while three were upstream of the apparent upstream territory boundary for 0998 and its assumed mate. Thus, the Dippers were dispersed along the available open stretch, and at approximately the same density as during the breeding season. One territory may have been maintained throughout the winter on a portion of the Sheep River that remained open. But I do not have sufficient data on the movements nor exclusiveness of the regions occupied by the Dippers to determine whether true, exclusive winter territories were established, as Bakus (1957) and Sullivan (1973) believed, or whether the birds simply maintained an inter-individual distance that moved with the bird (Price 1975).

The nature of breeding season territoriality in the study population seemed similar to that observed elsewhere for the American Dipper (Bakus 1957, Sullivan 1973, Price 1975) and was quite distinct from the relatively subdued aggression observed for European Dippers by Shooter (1970). Interspecific territoriality also was much highet for the Dippers in the southern Alberta population than reported by Sullivan (1973), or by Shooter (1970) for the European Dipper. Dippers in the Alberta population were extremely aggressive towards Spotted Sandpipers (_Actitis macularia_), particularly if there was a nest of a Spotted Sandpiper within the Dipper's territory. During one observation period at the Bridge Falls territory, male 0920 chased Spotted Sandpipers for short distances a total of seven times. Dippers were also observed on a few occasions to sing briefly at Robins (Turdus migratorius), Townsend's Solitaires, Western Flycatchers, and Swainson's Thrushes (Catharus ustulatus).

Population ecologists have only recently been conducting controlled, adequately monitored removal experiments to determine the presence or absence of surplus animals that are prevented from breeding by established individuals. The outcome of these types of experiments on bird species have shown that some populations may have surpluses (Harris 1970, Krebs 1971, Zwickel 1972, Bendell et al. 1972, Knapton and Krebs 1974) and others may not (Cederholm and Ekman 1976).

Klomp (1972) restates five conditions (first formulated by Watson and Moss 1970) that must be met before regulation of numbers can be attributed to territorial behaviour, that is, the presence of an excluded surplus of non-breeders. I examined each of these conditions in light of the apparent surplus (see p. 52) of Dippers (potentially non-breeding) in the Sheep River study area.

The first condition is that part of a population of potential settlers initially present on an area is inhibited from breeding in that area. There were more individuals on the Sheep River study area in the spring of 1976 than initiated breeding (Table 4). Several banded individuals were observed attempting to establish territories, and a number of pairs moved in to replace pairs I removed (Table

29). There was a temporary response to removal by adjacent territory holders; both 0920 and 4418 were observed in the adjacent downstream removal territories after removals. However, they did not defend these additional areas. Although I observed occasional unbanded, unestablished Dippers on the study area, there were no non-breeding individuals consistently observed. Price and Bock (1973) also could not find a non-breeding surplus residing on their study area, and suggested that transients continued to look for available nesting habitat throughout the season.

The second condition is that such non-breeders be physiologically capable of breeding when filling a vacancy created by the removal of established residents. One replacement pair on the Sheep River was permitted to breed and was successful. In addition, the gonads of replacement pairs were well developed which showed that these apparently excluded birds were capable of breeding.

The third condition is that breeding animals not completely use up any resource. If they are, then that resource is limiting. Space, food and nesting sites are generally proposed as potentially exhaustable resources (Klomp 1972) as the population density increases. Space, despite the mobility of Dippers, was not likely to be limiting numbers in the south Alberta population which suggests that space, per se, was not limiting. The mean length of territories in the Sheep River area was significantly greater (t-test, $p>0.05$) than that reported for monogamous Dippers in Boulder, Colorado (Price 1975). Therefore, in other areas Dippers were more densely packed than in the present study.

Price (1975) found that Dipper distribution throughout the year was often correlated with the abundance of food, however, size of territory was not. I also found that size of breeding territory was not correlated with abundance of benthic biomass (Spearman's rank correlation test, $p>0.1$; Fig. 21). I further examined the benthic biomass samples to determine whether certain components of the stream bottom fauna were correlated with territory length. Stomach analysis indicated that the orders Trichoptera, Ephemeroptera, and Plecoptera were important components of the diet of the Dipper (pp. 116-121), while other taxa found in the stream were negligibly represented. I found no correlation between size of territory and any or all three of the components of the stream bottom samples formed by the above three orders during the establishment of territories by the Dippers (Spearman's rank correlation test, $p>0.1$).

Dippers change feeding habits during floods when the water is exceedingly turbid and the number of possible foraging maneuvers is reduced (Sullivan 1973, Price 1975, this study). Only after particularly severe and prolonged floods in which extreme reductions of the original fauna have occurred (perhaps as low as 10%, Jones 1951) or after excessive and unnatural siltation has occurred (Price 1975), does it seem likely that food may be limiting. In the Sheep

River study area nest site availability fluctuated considerably from one portion of the stream to another (Fig. 9), however, within several km of stream there were unused nest sites (Table 28).

The last two conditions presented deal with long-term limitation of numbers. Condition four is that "the mortality or depressed recruitment due to the limiting factor(s) changes in an opposite sense to, and at the same rate as other causes of mortality or depressed recruitment". Condition five is that if all other conditions "are fulfilled and the numbers change following changes in food, then food and behaviour are both limiting the breeding population" (Klomp 1972). Without several years of field study, including observation of the effects of natural fluctuations of food or artificial enhancement of available food, one cannot adequately determine if these last two criteria hold for a population. However, because they represent long term approaches, one might look upon them as refinements. The first three conditions are, therefore, most important in determining the presence or absence of a group of individuals that are prevented from breeding by established residents.

The Sheep River area is typical of foothill streams (Miller 1962); there is marked heterogeneity in distribution of available nesting sites (Fig. 9) and food (Figs. 14-16). The stream system as it relates to Dippers can be compared with models of avian habitat distribution in a rather unique way. Pretwell and Lucas (1970) and Brown (1969) present models of the effect of territoriality on the distribution of birds in habitats of different quality. In their models birds are shown to settle in optimal breeding habitat first and then in sub-optimal breeding habitat. Fretwell and Lucas incorporate an additional feature into their model in that the quality of the habitat is partially dependent upon the density of residents. In other words, optimal habitat may reach a sub-optimal quality level by virtue of the presence of a number of territorial residents, at which point birds will settle in sub-optimal quality habitat. Eventually a point is reached where the density in this lower quality habitat is such that the quality levels, based upon a combination of habitat parameters and bird density, are the same for both habitat types and the birds move into each habitat at the same rate, presumably until the minimum territory size is reached for the particular habitat.

Dippers breed in spatially simple but structurally heterogeneous habitats. One part of a stream may be at a different level of habitat quality than an adjacent part. Conceptually, Dipper populations can be compared with these models. However, to fit the models accurately, one would need more precise delineation of habitat quality and observation of differential mortality in habitats of different quality. Such quantification is exceedingly difficult to obtain, and would require studies in extensive areas for such widely dispersed birds as Dippers. Price

(1975) reached a similar conclusion regarding his study population.

Krebs (1971) found that removal of Great Tits in optimal habitats, with respect to breeding success, resulted in replacement by mostly first-year individuals, from habitats that were suboptimal with respect to breeding success. He concluded that although his results indicated that territoriality influenced density, the function of territoriality in an evolutionary sense is probably spacing out of breeding pairs (defense against predators). Although his conclusion suggested that territorial behaviour was not a density-dependent factor regulating population size, the same reasoning implies that territorial behaviour can act as such a regulating mechanism in Dippers. The unused nest sites in the Sheep River study area were shown to be generally more accessible than used sites. With population density reaching the point where all of the preferred sites were taken, then one can see how territorial behaviour could function in spacing out to reduce predator access to nests and also where the population numbers in that area may be regulated in a density-dependent fashion.

Discussion of the existence of a surplus must be made in light of the occurrence of polygyny discovered by Price and Bock (1973) and for European Dippers by Mork (1975). The breeding success of polygynous birds fell below that of monogamous birds in the last year of Price's study. Nonetheless, such birds represented an opportunity for at least females among the excluded birds to take part in breeding. However, from Price's estimates of Dippers attempting to breed and being chased off it is unlikely that the entire group of excluded female Dippers were able to breed. On Gorge Creek I observed what might have been an instance of incipient polygyny, but unfortunately all three birds abandoned the nests. No other instances that approached polygyny were observed, despite the occurrence of several territories without adjacent territories on one side - the situations in which Price found all of his polygynous birds, and predicted as suitable locations for polygyny (Price and Bock 1973).

It appears then that in this study area the number of Dippers able to breed was limited by territorial behaviour while ultimately the availability of nest sites may be the limiting factor. Also, polygynous matings may, in general, be rarer than Price (1975) found and predicted for populations of Dippers in the Eastern Slopes of the Rocky Mountains.

CONCLUDING DISCUSSION

My objectives in carrying out this study were: to assess the availability and use of nest sites in an area where such sites were exclusively on natural substrate; to record the availability of food, its actual selection by Dippers in the breeding season, and the behavioural responses that may occur as a result of changing food availability or individual requirements; and to determine the effectiveness of social behaviour in preventing Dippers from breeding in a particular area.

In order to provide a framework for examining these topics, I presented an overview of population parameters of Dippers in the upper Sheep River basin, Alberta. Breeding distribution, nesting chronology, natality and mortality were found to be similar to other populations of the American Dipper and to species of Cinclus in general. A larger proportion of the Dipper population migrated than in any of the populations previously studied, which is linked with the drastic reduction in available habitat in the area during the winter. Dispersal, a critical part of the population dynamics of any species, remains poorly understood and is an area where further investigation would be fruitful, particularly in light of the presence of a surplus, non-breeding component of the population (see below).

Nest sites and cliff faces with ledges suitable for nest sites were clumped in distribution; certain portions of the main river in the study area had abundant nest sites while the two major tributaries appeared to have a dearth of suitable sites. Factors involved in use of nest sites were: selection (shown to depend upon level of stream noise, accessibility, substrate stability, and distance to nearest fast water); timing of establishment and extent of territories; and also nest site fidelity.

Food availability remained at about the same level throughout the summer with a slight decline in June. It is suggested that the constant availability of food and the abundance of cover on this study area enabled resident breeding Dippers to remain on territories during the moulting period, in contrast to other study populations where at least one of these resources was reduced. The selection of food, as determined by forage ratios, by breeding Dippers indicated a preference for the more conspicuous, larger benthic invertebrates. Flying adults of benthic immatures were also important in the diet. Terrestrial invertebrates made up a small portion of the diet as well. Fish were not commonly eaten by Dippers during this study and may be a very small part of their diet in general.

Dippers have a wide variety of foraging maneuvers and seem to show differences in use of certain maneuvers that vary with the type of stream habitat found in different territories and within territories between individuals. The foraging ecology of Dippers is an area where further investigation would be fruitful, particularly in regard to predation models.

Through removal experiments, I showed that a surplus of non-breeding Dippers existed in the Sheep River area. Territorial behaviour of resident individuals was considered to be involved in causing exclusion of these birds. Observations of at least 2-year old birds seeking territories on the study area were noted as further evidence, because of site fidelity of these birds, that non-breeding birds occurred in this population. I reviewed Klomp's (1972) criteria for determination of the occurrence of a surplus excluded by social behaviour. I believe that the Dipper population met all of the short term criteria, although longer term work would be required to determine the constant presence of a surplus.

The ultimate question appears then to be why do surpluses of Dippers occur, mediated by territorial behaviour? In most sections of streams where Dippers reside, even in natural areas like the present study, there are adequate nest sites and food supply. Given the drastic effect that periodic floods have upon nest success, through both nest damage and reduction of benthic biomass available as food, it would be adaptive for Dippers to defend a territory which would include a sufficient quantity of these resources to either renest or find sufficient food for the young, respectively. These may be the ultimate factors which underly the proximate mechanism of territorial behaviour in determining breeding population numbers.

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APPENDIX 1 Banding data and measurements for all Dippers banded during 1975 and 1976 in the Sheep River study area, Alberta.

No.	Date	Band no.[1]	Colour bands[2]	Age[3] and sex	Stream location[4]		Length (mm) wing	tarsus	Wt. (g)
	1975								
1	19-4	0901	R/- S/-	A F	Sheep	41.6	87.0	29.3	54.5
2	27-4	0902	W/- S/-	A F	Sheep	37.9	88.0	29.4	52.5
3	27-4	0903	B/- S/-	A M	Sheep	37.9	93.0	31.7	58.5
4	28-4	0904	G/- S/-	A M	Sheep	0.2	89.0	31.0	55.0
5	28-4	0905	Y/- S/-	A M	Sheep	7.8	90.5	30.8	62.0
6	28-4	0906	R/- R/S	A M	Sheep	7.8	95.0	29.4	60.0
7	29-4	0907	R/- S/W	A F	Sheep	16.5	83.0	28.4	52.0
8	2-5	0908	B/- S/B	A M	Sheep	41.6	87.0	30.4	56.5
9	2-5	0909	W/G S/-	A M	Sheep	51.5	95.0	30.6	60.0
10	2-5	0910	G/R S/-	A F[5]	Sheep	51.5	86.0	29.5	54.0
11	3-5	0911	R/Y S/-	A M[5]	Sheep	77.5	90.0	30.5	60.0
12	3-5	0912	R/B S/-	A M	Sheep	74.0	94.0	31.2	64.0
13	3-5	0913	R/W S/-	A M[5]	Sheep	1.0	92.0	31.7	63.0
14	3-5	0914	Y/W S/-	A F[5]	Sheep	1.0	85.0	28.1	53.0
15	8-5	0915	G/B S/-	A F	Sheep	3.0[6]	90.0	29.7	50.0
16	8-5	0916	G/Y S/-	A M	Sheep	2.6	95.0	29.1	56.0
17	9-5	0917	R/G S/-	A F	Sheep	51.0	90.0	29.3	59.0
18	9-5	0918	B/Y S/-	A F[5]	Sheep	51.0	83.0	29.8	49.5
19	9-5	0919	O/O S/-	A F[5]	Sheep	48.5	86.0	28.7	51.0
20	15-5	0920	Y/B S/-	A M	Sheep	46.2	88.0	30.2	56.0
21	15-5	0921	Y/R S/-	A M[5]	Sheep	46.2	93.0	30.6	60.0
22	15-5	0922	R/- S/R	A M	Sheep	37.5	90.0	30.4	57.5
23	23-5	0923	G/- S/G	A F	Dyson	43.5	85.0	28.4	50.0
24	23-5	0924	R/R S/-	A M	Dyson	43.5	94.0	30.8	61.5
25	25-5	0925	Y/- S/G	A F	Gorge	24.4	87.0	28.7	52.5
26	26-5	0926	O/- S/O	A M	Gorge	39.8	90.0	29.7	53.5
27	26-5	0927	Y/- S/R	A M	Dyson	5.0	98.5	31.0	62.0
28	26-5	0928	G/- S/B	A F	Dyson	5.0	89.0	27.9	50.0
29	29-5	0929	W/- S/W	A F[5]	Dyson	26.2	86.5	28.4	49.5
30	29-5	0930	B/B S/-	A M[5]	Dyson	26.2	92.0	29.4	56.0
31	29-5	0931	-/- O/S	A F	Dyson	36.5	85.0	29.1	56.0
32	5-6	0932	B/R S/-	A F	Sheep	96.9	86.0	29.5	54.5
33	7-6	0934	B/G S/-	A F	Gorge	68.4	86.0	29.0	53.5
34	7-6	0935	-/- S/G	A M	Gorge	68.4	91.0	31.4	56.5
35	8-6	0936	B/- B/S	A F	Gorge	39.5	86.0	28.3	62.5
36	24-6	0937	W/W S/R	A F	Sheep	130.6	81.0	28.9	51.0
37	25-6	0938	B/B S/B	N -	Sheep	96.9			
38	25-6	0939	B/B S/R	N -	Sheep	96.9			
39	6-7	0940	O/R S/B	N -	Dyson	44.6			
40	6-7	0941	O/B S/O	N -	Dyson	44.6			
41	6-7	0942	O/O S/R	N -	Dyson	44.6			
42	6-7	0943	B/O S/R	N -	Dyson	44.6			
43	6-7	0944	Y/Y S/O	N -	Dyson	36.4			
44	6-7	0945	Y/Y S/B	N -	Dyson	36.4			
45	6-7	0946	O/Y S/B	N -	Dyson	36.4			
46	6-7	0947	Y/O S/R	N -	Dyson	36.4			

APPENDIX 1 cont.

No.	Date	Band no.[1]	Colour bands[2]	Age[3] and sex	Stream location[4]	Length (mm)		Wt. (g)
						wing	tarsus	
47	6-7	0949	R/O S/G	N -	Dyson 4.7			
48	6-7	0950	G/O S/B	N -	Dyson 4.7			
49	6-7	0951	G/G S/B	N -	Dyson 4.7			
50	6-7	0952	G/G S/O	N -	Dyson 4.7			
51	9-7	0953	R/B S/B	N -	Sheep 37.3			
52	9-7	0954	W/R S/O	N -	Sheep 37.3			
53	9-7	0955	B/R S/R	N -	Sheep 37.3			
54	10-7	0956	W/B S/R	A F	Sheep 82.6	88.0	30.4	53.0
55	11-7	0957	Y/Y S/Y	A F	Sheep 68.5	89.0	28.5	58.0
56	11-7	0958	B/W S/R	N -	Sheep 86.8			
57	11-7	0959	W/W S/O	N -	Sheep 86.8			
58	11-7	0960	W/O S/R	N -	Sheep 86.8			
59	11-7	0961	W/W S/W	N -	Sheep 86.8			
60	12-7	0962	G/O S/R	N -	Gorge 24.1			
61	12-7	0963	G/W S/O	N -	Gorge 24.1			
62	12-7	0964	G/W S/B	N -	Gorge 24.1			
63	12-7	0965	G/O S/Y	N -	Gorge 24.1			
64	12-7	0966	G/O S/O	N -	Gorge 24.1			
65	16-7	0967	G/O S/G	N -	Sheep 119.4			
66	16-7	0968	G/B S/G	N -	Sheep 119.4			
67	18-7	0969	R/B S/G	N -	Sheep 15.3			
68	18-7	0970	R/B S/W	N -	Sheep 15.3			
69	18-7	0971	R/B S/R	N -	Sheep 15.3			
70	20-7	0972	R/B S/O	A F	Sheep 109.9	88.0	29.3	52.5
71	24-7	0973	R/O S/O	N -	Junct. 18.0			
72	24-7	0974	R/O S/B	N -	Junct. 18.0			
73	25-7	0975	G/R S/O	N -	Sheep 51.2			
74	25-7	0976	G/R S/R	N -	Sheep 51.2			
75	25-7	0977	G/R S/G	N -	Sheep 51.2			
76	25-7	0978	G/R S/B	N -	Sheep 51.2			
77	29-7	0979	B/R S/G	N -	Sheep 110.8			
78	29-7	0980	G/R S/W	N -	Sheep 110.8			
79	29-7	0981	B/R S/O	N -	Sheep 110.8			
80	29-7	0982	B/R S/B	N -	Sheep 110.8			
81	29-7	0983	B/R S/W	N -	Sheep 110.8			
82	29-7	0985	G/B S/B	N -	Sheep 45.2			
83	29-7	0986	G/B S/O	N -	Sheep 45.2			
84	2-8	0987	B/W S/B	N -	Gorge 9.0			
85	2-8	0988	B/W S/W	N -	Gorge 9.0			
86	2-8	0989	W/R S/R	A F	Gorge 9.0	82.0	29.0	48.5
87	3-8	0990	G/W S/G	N -	Gorge 68.5			
88	3-8	0991	G/B S/R	N -	Gorge 68.5			
89	3-8	0992	W/G S/W	N -	Sheep 135.2			
90	3-8	0993	W/G S/G	N -	Sheep 135.2			
91	3-8	0994	W/G S/R	N -	Sheep 135.2			
92	3-8	0995	W/G S/B	N -	Sheep 135.2			
93	13-8	0996	R/W S/W	A M	Sheep 136.0	97.0	30.9	63.0
94	16-9	0997	R/R S/B	A M[5]	Sheep 83.6	87.0[7]	30.4	65.0
95	16-9	0998	B/B S/G	A M	Sheep 88.2	93.0[7]	30.8	67.0

APPENDIX 1 cont.

No.	Date	Band no.[1]	Colour bands[2]	Age[3] and sex	Stream location[4]	Length (mm)		Wt. (g)
						wing	tarsus	
96	16-9	0999	W/W S/G	J M[5]	Sheep 91.5	92.0	30.5	66.0
97	16-9	1000	B/W S/G	U F[5]	Sheep 91.5	84.0	29.3	60.0
98	19-9	4401	W/W S/B	A M	Sheep 119.6	87.0[7]	30.8	65.0
99	19-9	4402	W/B S/G	J F[5]	Sheep 110.5	84.0	29.3	53.0
100	19-9	4403	W/R S/W	A ?	Sheep 110.5	91.0	29.4	
	1976							
101	26-5	4404	B/B S/Y	A F	Gorge 4.0	85.2	28.4	59.0
102	26-5	4405	L/L S/R	A M	Gorge 4.0	94.0	31.8	62.0
103	12-4	4406	R/W S/G	A M[5]	Gorge 0.3	92.2	29.5	56.5
104	12-4	4407	R/G S/Y	A F[5]	Gorge 0.3	85.2	28.2	52.0
105	15-4	4408	W/R S/B	A F	Sheep 51.5	83.8	28.0	52.5
106	18-4	4409	R/W S/B	A F[5]	Sheep 41.8	86.0	29.1	52.0
107	18-4	4410	R/R S/G	A F	Sheep 41.8	85.0	29.6	56.0
108	23-4	4411	B/G S/O	A F	Sheep 70.6	84.3	27.7	56.0
109	24-4	4412	R/G S/R	A F	Sheep 87.0	88.0	28.3	49.0
110	25-4	4413	R/W S/R	A F	Sheep 110.5	84.8	27.9	52.0
111	26-4	4414	L/L S/L	A M	Sheep 36.7	90.8	30.1	59.0
112	1-5	4415	P/G S/B	A M	Sheep 65.5	90.0	30.3	58.0
113	8-5	4416	W/R S/G	A M[5]	Sheep 104.9	91.3	30.6	64.0
114	15-5	4417	B/B S/O	A M[5]	Sheep 36.7	86.3	30.7	57.0
115	19-5	4418	B/G S/B	A ?	Sheep 109.5	86.0	30.4	56.0
116	19-5	4419	R/G S/G	A F[5]	Sheep 109.5	88.0	27.9	61.0
117	21-5	4420	B/G S/Y	A M	Gorge 6.7	92.8	31.0	61.0
118	28-5	4421	Y/Y S/G	A M	Gorge 24.5	89.3	30.8	59.0
119	28-5	4422	O/W S/B	A F	Gorge 24.5	83.0	27.7	53.0
120	29-5	4423	O/L S/Y	A ?	Gorge 74.0	88.8	30.0	52.0
121	29-5	4424	G/W S/R	A F	Gorge 74.0	84.8	29.1	53.0
122	29-5	4425	L/L S/W	A M	Dyson 35.7	95.2	29.3	64.0
123	2-6	4426	W/O S/B	A M	Gorge 78.7	93.7	31.6	62.0
124	4-6	4427	L/G S/L	A F	Sheep 15.3	80.0	28.6	52.0
125	8-6	4428	L/R S/B	A F	Gorge 24.7	85.2	29.5	
126	9-6	4429	R/R S/Y	A M	Dyson 22.0	91.0	30.3	61.0
127	9-6	4430	O/L S/B	A M[5]	Dyson 22.0	92.2	30.2	57.0
128	17-6	4431	R/R G/S	N -	Sheep 51.4			
129	17-6	4432	W/W G/S	N -	Sheep 51.4			
130	17-6	4433	B/B G/S	N -	Sheep 51.4			
131	17-6	4434	L/L G/S	N -	Sheep 51.4			
132	18-6	4435	L/L L/S	N -	Sheep 45.2			
133	18-6	4436	Y/Y L/S	N -	Sheep 45.2			
134	18-6	4437	O/O L/S	N -	Sheep 45.2			
135	23-6	4438	B/B O/S	A F	Dyson 10.4	82.0	30.1	
136	28-6	4439	O/G R/S	N -	Sheep 15.3			
137	28-6	4440	O/B R/S	N -	Sheep 15.3			
138	29-6	4441	R/W B/S	N -	Gorge 4.8			
139	29-6	4442	R/L B/S	N -	Gorge 4.8			
140	29-6	4443	R/G B/S	N -	Gorge 4.8			
141	29-6	4444	R/R B/S	N -	Gorge 4.8			
142	29-6	4445	R/B B/S	N -	Gorge 4.8			
143	30-6	4446	L/L Y/S	N -	Dyson 44.7			

APPENDIX 1 cont.

No.	Date	Band no.[1]	Colour bands[2]	Age[3] and sex	Stream location[4]	Length (mm) wing	tarsus	Wt. (g)
144	30-6	4447	L/R Y/S	N -	Dyson 44.7			
145	30-6	4448	L/G Y/S	N -	Dyson 44.7			
146	30-6	4449	L/B Y/S	N -	Dyson 44.7			
147	30-6	4450	L/Y Y/S	N -	Dyson 44.7			
148	30-6	4451	L/B R/S	N -	Gorge 39.5			
149	30-6	4452	L/G R/S	N -	Gorge 39.5			
150	30-6	4453	L/Y R/S	N -	Gorge 39.5			
151	30-6	4454	L/L R/S	N -	Gorge 39.5			
152	30-6	4455	B/Y O/S	N -	Dyson 26.8			
153	30-6	4456	B/G O/S	N -	Dyson 26.8			
154	30-6	4457	B/R O/S	N -	Dyson 26.8			
155	30-6	4458	B/L O/S	N -	Dyson 26.8			
156	30-6	4459	B/O O/S	N -	Dyson 26.8			
157	4-7	4460	L/B R/S	N -	Gorge 24.0			
158	4-7	4461	L/G R/S	N -	Gorge 24.0			
159	4-7	4462	L/Y R/S	N -	Gorge 24.0			
160	4-7	4463	L/L R/S	N -	Gorge 24.0			
161	5-7	4464	L/R L/S	N -	Gorge 9.3			
162	5-7	4465	L/O L/S	N -	Gorge 9.3			
163	5-7	4466	L/B L/S	N -	Gorge 9.3			
164	5-7	4467	L/G L/S	N -	Gorge 9.3			
165	7-7	4468	Y/R R/S	N -	Dyson 10.2			
166	7-7	4469	Y/G R/S	N -	Dyson 10.2			
167	7-7	4470	Y/Y R/S	N -	Dyson 10.2			
168	7-7	4471	Y/B R/S	N -	Dyson 10.2			
169	8-7	4472	G/G L/S	N -	Cliff 8.0			
170	8-7	4473	G/R L/S	N -	Cliff 8.0			
171	8-7	4474	G/B L/S	N -	Cliff 8.0			
172	8-7	4475	G/Y L/S	N -	Cliff 8.0			
173	8-7	4476	G/O L/S	N -	Cliff 8.0			
174	9-7	4477	W/R B/S	N -	Sheep 63.8			
175	9-7	4478	W/G B/S	N -	Sheep 63.8			
176	18-7	4479	O/L R/S	A F	Sheep 16.0[6]	82.2	28.4	
177	19-7	4480	W/B B/S	A M	Sheep 36.8	90.0	31.0	
178	19-7	4481	L/R B/S	A F	Sheep 36.8	85.8	29.5	
179	27-7	4482	L/L B/S	N -	Sheep 18.0[6]			
180	27-7	4483	L/Y B/S	N -	Sheep 18.0[6]			
181	27-7	4484	L/G B/S	N -	Sheep 18.0[6]			
182	27-7	4485	L/B B/S	N -	Sheep 18.0[6]			
183	28-7	4486	W/L B/S	J -	Sheep 18.0[6]			
184	28-7	4487	L/G G/S	N -	Sheep 37.1			
185	28-7	4488	L/R G/S	N -	Sheep 37.1			
186	28-7	4489	L/B G/S	N -	Sheep 37.1			
187	28-7	4490	L/Y G/S	N -	Sheep 37.1			
188	2-8	4491	B/R Y/S	J -	Burns			
189	2-8	4492	B/L Y/S	J -	Burns			
190	2-8	4493	B/Y Y/S	J -	Burns			

[1] These are the last 4 digits of the official band number and are used within the text to refer to individuals.
[2] The colours used were: R -red, B -light blue, G -dark green, W -white, Y -yellow, O -orange, L -light green, and S -silver (the metal official band).
[3] The age classes used were: A -adult, N -nestling, J -juvenile (less than 1 year old), U -unknown.
[4] The location is given in 100 m units upstream from the mouth on each creek or upstream from the mouth of Gorge Creek for birds on the Sheep River.
[5] Sex determined using analysis (Appendix II).
[6] Denotes locations of birds on Sheep River in 100 m units downstream from the mouth of Gorge Creek.
[7] These wing measurements are from birds in moult.

APPENDIX II

Sex Determination of Dippers

As an aid in determining the sex of Dippers I obtained measurements of left wing chord, lengths of right tarsus and exposed culmen, and body weight of all adults banded. Andersson and Wester (1971, 1972) showed that 99% of all *C. c. cinclus* could be separated into sexes on the basis of wing length alone. The means of tarsus and culmen lengths were also significantly different, however, considerable overlap in these parameters occurred between the two sexes. They showed that the difference in mean weight of the two sexes (10.8 g) was highly significant; males were larger than females. Richter (1953) stated that, in *C. c. aquaticus*, females have wing lengths less than 89 mm and males have wing lengths greater than 90 mm. Creutz (1966) mentioned that *C. c. cinclus* have an average weight of about 60 g, while *C. c. aquaticus* males range from 58 to 75 g and females range from 50 to 67 g.

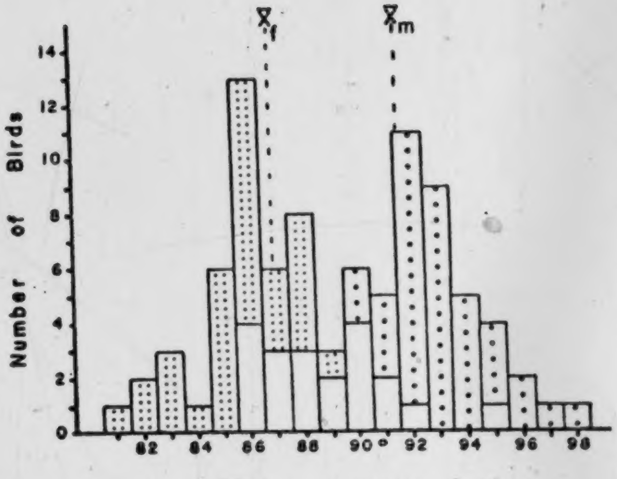
Price (1975) stated that wing length can be used to separate the sexes of *C. mexicanus* but does not present any data to support this statement. Godfrey (1966) showed that the means of the wing lengths were different for male and female *C. mexicanus*, but also that there is considerable overlap in this measurement.

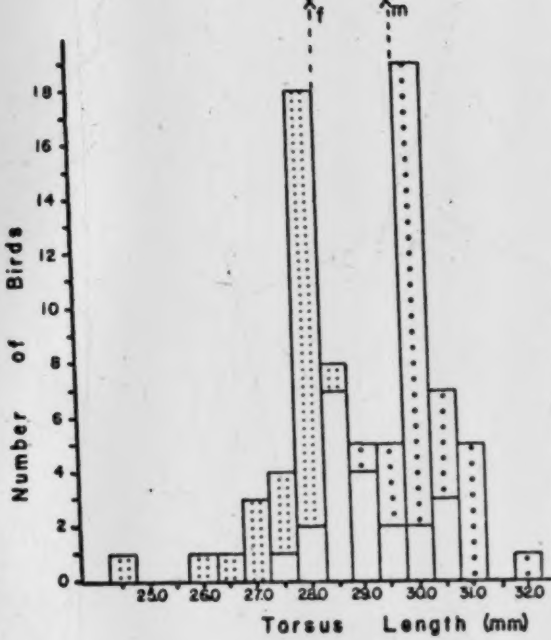
After banding adult Dippers, I measured the wing length to the nearest 0.5 mm using a plastic ruler, and the tarsus and culmen lengths to the nearest 0.1 mm using a vernier caliper. I also weighed the birds to the nearest 0.05 g using a Pesola spring scale, while they were confined in a plastic museum tube. In addition, I measured wing, tarsus and culmen lengths of 105 Dipper specimens borrowed from several museums (Thomas Burke Memorial Washington State Museum, University of Washington; Royal Ontario Museum, Toronto; Bird and Mammal Museum, University of Montana; Museum of Natural History, The University of Kansas; Department of Zoology, Vertebrate Museum, University of British Columbia; Zoology Museum, Oregon State University; British Columbia Provincial Museum, Victoria; Museum of Vertebrate Zoology, University of California, Berkeley).

There was considerable overlap (84% wing, 88% tarsus, 97% culmen) between male and female museum specimens (Fig. 22) although it was least for the wing length. Mean lengths of wing and tarsus were found to be significantly different between the two sexes ($t=8.99$, $p<0.0005$; and $t=7.21$, $p< 0.0005$, respectively). Culmen mean lengths were also significantly different between the two sexes ($t=2.48$, $0.025>p>0.01$), but overlap was 13 and 9% more than for wing lengths and tarsus lengths, respectively.

There is somewhat less overlap (32% wing, 50% tarsus, 96% culmen, and 67% weight) among live birds of known sex (Fig. 23) than for the museum specimens. The broad geographical distribution represented in the latter group may explain the greater overlap. This hypothesis is

Figure 22. Distributions of wing, tarsus, and culmen lengths for 105 museum skins of Dippers. Close stippling indicates number of females, large dots indicate number of males, and the blank sections are regions of overlap. Means for each sex are indicated for all three measurements.


$\bar{X}_f$
$\bar{X}_m$
Number of Birds
0
2
4
6
8
10
12
14
82
84
86
88
90
92
94
96
98
Wing Length (mm)


$\bar{X}_f$
$\bar{X}_m$
Number of Birds
0
2
4
6
8
10
12
14
16
18
25.0
26.0
27.0
28.0
29.0
30.0
31.0
32.0
Torsus Length (mm)

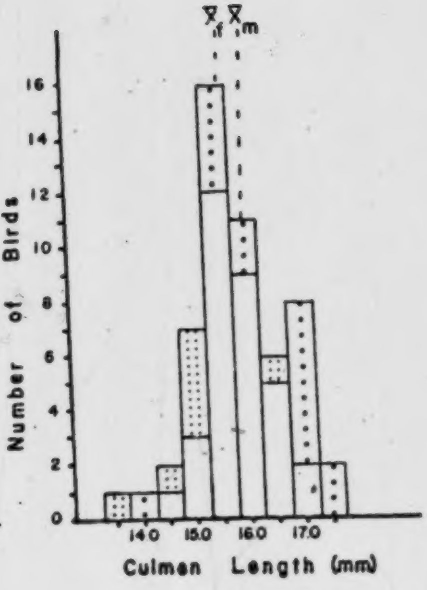
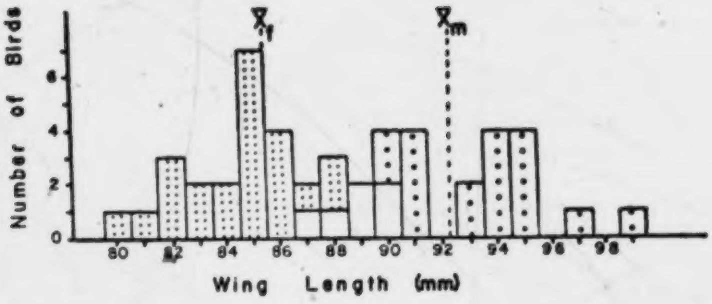
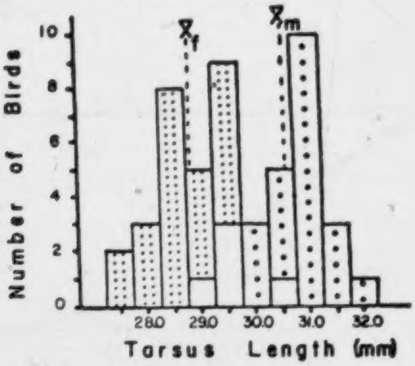
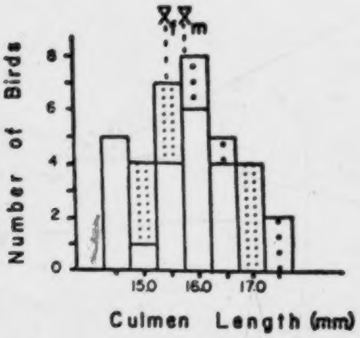
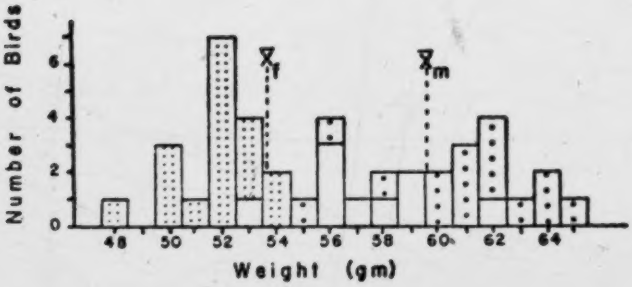

$\bar{X}_f$
$\bar{X}_m$
Number of Birds
0
2
4
6
8
10
12
14
16
14.0
15.0
16.0
17.0
Culmen Length (mm)

Figure 23. Distributions of wing, tarsus, and culmen lengths, and body weights for 56 Dippers banded and sex determined on the Alberta study area. Close stippling indicates number of females, large dots indicate number of males and the blank sections are regions of overlap. Means for each sex are indicated for all four measurements.


$\bar{X}_f$
$\bar{X}_m$
Number of Birds
0
2
4
6
80
82
84
86
88
90
92
94
96
98
Wing Length (mm)


$\bar{X}_f$
$\bar{X}_m$
Number of Birds
0
2
4
6
8
10
28.0
29.0
30.0
31.0
32.0
Tarsus Length (mm)


$\bar{X}_f$ $\bar{X}_m$
Number of Birds
0
2
4
6
8
15.0
16.0
17.0
Culmen Length (mm)


$\bar{X}_f$
$\bar{X}_m$
Number of Birds
0
2
4
6
48
50
52
54
56
58
60
62
64
Weight (gm)

supported by the observation that the mean wing lengths were different, but not significantly different for the same sexes between Dippers from a Trinity County, California (Fig. 1) population and a Boulder, Colorado population (Marilee Coriell pers. comm.). In the southern Alberta population, the wing lengths overlapped considerably more than in either of these latter populations (0% California, 9% Colorado); this difference may be because of the poorly representative sample size of birds measured in the California population (six males, eight females) and the unequal representation of the sexes measured from the Colorado population (10 males, 38 females). I measured an approximately equal number of both sexes (23 males, 25 females).

Although all of the measurements obtained showed a difference between males and females, I could not positively identify most birds of unknown sex using just one test criterion. However, it appeared that a combination of all criteria, except the culmen length, could be useful in discriminating between the two sexes. To test whether a multivariate approach might be useful, I used a Hotelling's T^2 test (Tatsuoka 1971). This test shows whether or not these criteria (measurement of wing, tarsus, and body weight) contributed to the difference between the two groups (sexes). The advantages of Hotelling's T^2 test over simple t-tests are (1) it protects against making type I error; if one were to do several t-tests instead of one T^2 test, then there is a greater chance of a significant result occurring simply by chance, and (2) it removes correlations between test criteria in calculating the final T^2 statistic; several t-tests might show significant differences, which are related to a common underlying factor; therefore, there should only be one indicator of difference. The test supported the hypothesis that these three criteria (wing length, tarsus length, body weight) were suitable for discriminating between the sexes ($p<0.01$ for all three criteria).

The wing lengths overlapped between the sexes less than the tarsus lengths and body weights. I chose to compare wing length with tarsus length and with body weight in simple graphs (Figs. 24, 25) to determine whether I could discriminate between the sexes and identify birds of unknown sex. There were definite spatial clumpings representing a group of males and a group of females. However, there was still considerable overlap between the values. Several birds of unknown sex (30%) remained unclassifiable.

A multivariate discriminant function provides a statistical method for discriminating between sexes and simultaneously including a confidence interval to reduce the chance of misclassifying a bird. To apply a discriminant function, the data must be normally distributed and the variances equal (Tatsuoka 1971). The matrices formed from the values of the test criteria were found to have a homogeneous dispersion, that is they did not have

Figure 24. Tarsus lengths compared with wing lengths of all banded adult Dippers on the Alberta study area, for sex determination of individuals not observed breeding. Triangles indicate known female adults; solid squares indicate known male adults, and circles indicate unknown sex birds.

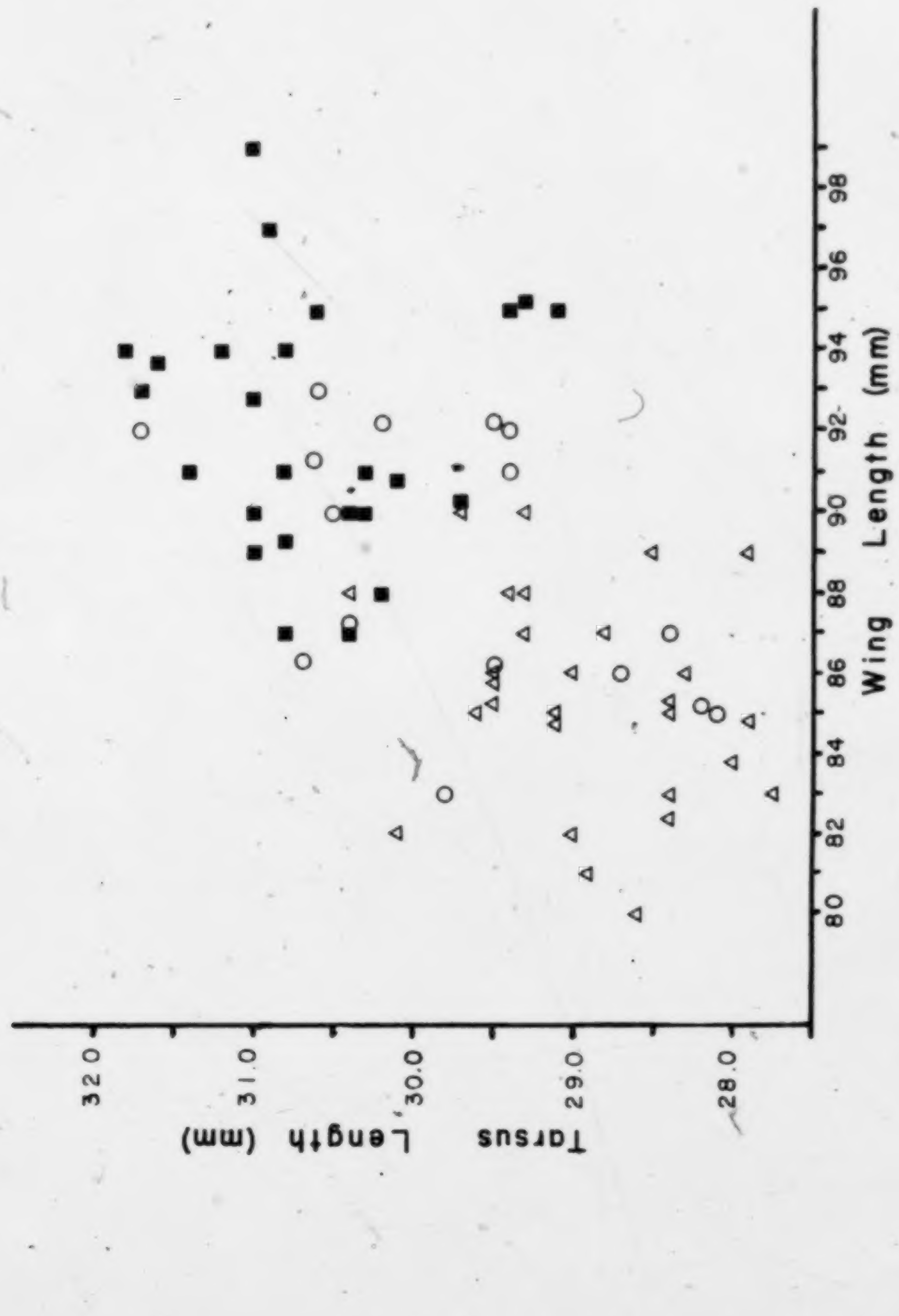
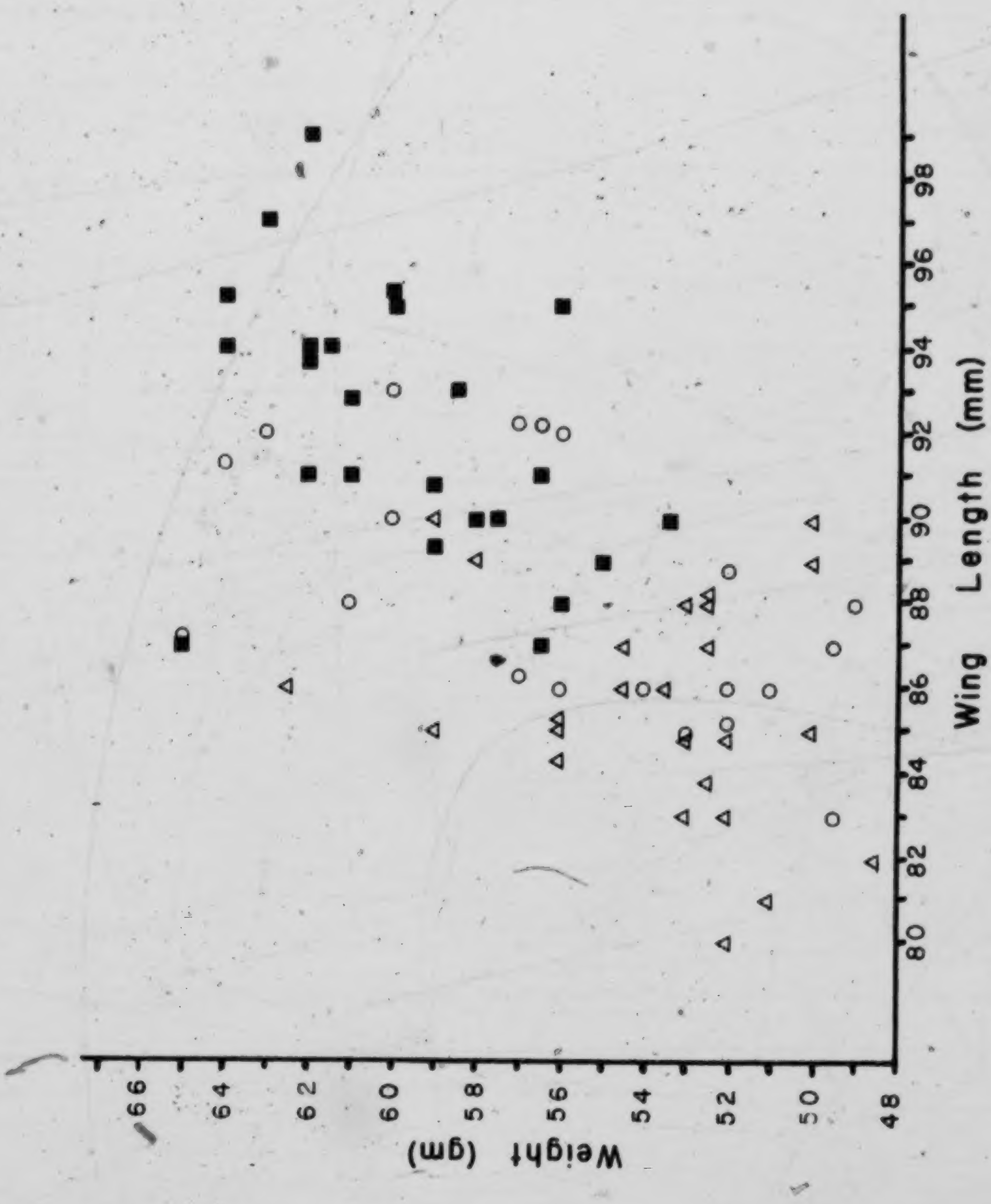

Tarsus Length (mm)
32.0
31.0
30.0
29.0
28.0
Wing Length (mm)
80
82
84
86
88
90
92
94
96
98

Figure 25. Weights compared with wing lengths of all banded adult Dippers on the Alberta study area, for sex determination of individuals not observed breeding. Triangles indicate known female adults, solid squares indicate known male adults, and circles indicate known sex birds.


Weight (gm)
66
64
62
60
58
56
54
52
50
48
Wing Length (mm)
80
82
84
86
88
90
92
94
96
98

significantly different dispersions ($X^2 = 9.17$, 6 df; $0.25>p>0.10$). Therefore, a discriminant function could be applied to these data. I used two discriminant functions: one function with three test criteria (wing length, tarsus length, body weight) and one function excluding weight. Weight was not included in the latter function because of variability associated with time since last foraging by the bird and also time of season. Andersson and Wester (1972) found significant diurnal and seasonal variation in weights of individual C. c. cinclus. In addition, the general utility of the discriminant function is increased if weight is excluded, because it is a measurement that is difficult to make when banding birds and is generally not available for museum specimens.

The discriminant analysis is based upon the calculation of a linear discriminant function, which in turn incorporates coefficients that reflect the relative contribution to the function of the test criteria used and which also takes the variance of the two populations into consideration. The linear function which I used to calculate discriminant scores was

$$L_i X_i$$

which is the linear function of the X_i (the variates or criteria chosen) that gives the smallest probability of misclassification, and the L_i which are coefficients that are calculated to meet this requirement (Snedecor and Cochran 1972). Using this function I calculated a discriminant score for each banded Dipper of known sex (computer program for calculation devised by Dr. B. Chernick, Dept. of Zoology, U. of Alberta). A boundary separating the scores for males from females was calculated and confidence boundaries were established above and below this separation point. The upper confidence boundary (Table 30) is the point below which 10% of the discriminant scores of the males fall. The lower confidence boundary (Table 30) represents the point above which 10% of the discriminant scores of the females fall. Discriminant scores were calculated for all Dippers of unknown sex, which were then classified as either male, female, or indeterminable (Table 30). I was able to classify 20 out of the 23 birds of unknown sex using these discriminant functions.

I examined the discriminant scores of the Dippers of known sex and found that only one bird (female 0956 with a discriminant score of 48.4424, from the discriminant function using only two criteria -see Table 30) would have been misclassified using the discriminant analysis. Therefore, I feel that the multivariate discriminant function analysis enables me to safely determine the sex of nearly all Dippers found in the Sheep River study area.

This type of analysis should enable sex determination of nearly all individuals in any study area, providing an initial sample of measurements of Dippers of known sex has been obtained. The probability of misclassifying

Table 30. Discriminant scores calculated using a multivariate discriminant function with three criteria (wing length, tarsus length, weight) or two criteria (wing length, tarsus length) for all Dippers of unknown sex caught on the Sheep River study area, Alberta.

	Three Criteria	Two Criteria	Sex[1] Denoted
Upper boundary	47.5813	48.3201	
Lower boundary	46.8302	47.6756	
Dippers of Unknown Sex			
0910	46.2819	47.1407	F
0911	48.4229	48.9760	M
0913	50.1251	50.5658	M
0914	44.7553	45.5775	F
0918	45.6236	46.7725	F
0919	45.2811	46.3725	F
0921	49.0239	49.7282	M
0929	44.9562	46.1937	F
0930	47.3991	48.3571	M
0997	48.2865	48.2237	M
0999	49.3210	49.4135	M
1000	46.3184	46.5111	F
4402	45.6679	46.5111	F
4403	-	48.1384	U
4406	47.5698	48.4969	M
4407	44.7867	45.7173	F
4409	45.7350	46.7566	F
4416	49.1062	49.3564	M
4417	47.6946	48.3587	M
4418	47.2799	48.0050	U
4419	45.8291	46.0417	F
4423	47.0239	48.0583	U
4430	48.2480	49.1691	M

[1] M-male, F-female, U-unknown sex.

individuals would be reduced if confidence boundaries were increased to 15% of the discriminant scores of birds of known sex; the level of 10% appears to be adequate for this study, but other users of this technique may wish to chose a different level.